TEMPORAL TRENDS IN A LARGE MARINE ECOSYSTEM

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Temporal Trends in a Large Marine Ecosystem

by

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Abstract

Different scales of change imply the need for different approaches to study change in ecosystems. I determined if proximate causes for ecosystem change are apparent at different biological and spatial scales by analyzing time series at fairly short temporal scales (< 30 years). I determined whether complex dynamics involving abundance could be described for a single species whose population units are distinctly defined, for two deep-sea species, and for the demersal fish community of the northeast Newfoundland-Labrador Shelf using two newer approaches of multivariate time series analysis: min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA). I analyzed trends in abundance and, for the demersal community, mean size and investigated the relationships between observed trends and external factors (environmental, exploitation and natural (non-human) predation) operating on time lags. No one factor fully explained fish population and community dynamics in the Northwest Atlantic, but rather a combination of factors operating over several temporal scales were largely responsible for the dynamics seen today. No one scale captures all the dynamics in abundance and mean size for populations, deep-sea species, or the fish community.

Before using the techniques on deep-sea species, I wanted to determine if the data were adequate to describe trends in "non-traditional" fishery species; for this, I used generalized linear models. I discovered several deep-sea species qualified as endangered. From that analysis arose questions regarding statistical rigor: does the loss of comprehensiveness bias results? I assessed several approaches to analyzing population

change that explicitly dealt with differing degrees of data filtering and the comprehensiveness of associated metrics with a detailed examination of two North Atlantic endemic deep-sea species, *Macrourus berglax* and *Coryphaenoides rupestris*. Statistical rigor is necessary, not to show that a trend exists in available data for deep-sea species, but to ensure that the trend is real. When assessing temporal trends under any conditions, ensuring the comparability of the index over time is extremely important.

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[i] Chapter titles are song titles from the Classic American Songbook and are a nod to my supervisor, R.L. Haedrich.

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[1]Chapter 1. I Can't Get Started: An Introduction to Change at Multiple Scales

1.1 Ecosystem change

Fishery science has shifted its focus from the dynamics of single populations to wide-ranging attempts to understand how entire ecosystems function. "Ecosystem-based management" has become a catch-phrase and a goal within fishery science, and large marine ecosystems (LMEs), most of which are fishery ecosystems, are the subject of a regular series of monographs and papers (Sherman et al. 1990, 1993, Sherman 1994, Larkin 1996). An ecosystem approach is not a definitive answer to fisheries problems, but instead represents a method of managing fishery resources in a way that does the least amount of damage to the ecosystem while providing sustainable employment opportunities and food yield. Humans and their influence on the ecosystem through activities such as fishing, pollution and habitat destruction, are also major players within the system and must not be forgotten or ignored (Ludwig et al. 1993). There is no one way to determine which approach will work for a particular system because each ecosystem is unique. In reality, determining what will not work for an ecosystem is probably much easier. The single species management approach appears to be currently working in a few cases (e.g., Breen and Kendrick 1997, Dewees 1998, Witherell et al. 2000, Matthíasson 2003), but for the most part, the literature argues that it does not (e.g., Radovich 1982, Hutchings and Myers 1994, Larkin 1996, Hutchings et al. 1997,

[1] Chapter titles are song titles from the Classic American Songbook and are a nod to my supervisor, R.L. Haedrich. Most chapters have been or are in the process of being published and, as such, have only the technical title.

Jakobsson and Stefánsson 1998, Hutchings 2000, Hilborn et al. 2003, Myers and Worm 2003, Rosenberg 2003a).

Ecosystems change continuously through time, exist at multiple temporal and spatial scales, and many of their characteristic interactions and processes operate on time lags (O'Neill et al. 1986). Interactions between all ecosystem components can occur on many spatial-temporal scales. As spatial scale increases, longer temporal processes become increasingly important in determining ecosystem functioning (Turner and Johnson 2001). Because ecosystems are a strongly interactive network of living organisms and physical components, a change in any one function, interaction, or component can create a cascade of changes throughout the system (Higashi and Burns 1991, Jackson et al. 2001). Perturbations, events that change resource pools or the physical environment, cause change by disrupting population, community, or ecosystem structure (White and Pickett 1985). A system's response to a perturbation is complex because perturbations can occur simultaneously, be physical or biological in origin, act on the system from within or without, and span a range of spatial and temporal scales (Jørgensen 2002).

Ecosystems are constantly reacting to change and the effects of change can be direct, indirect, or integrated into the system (Ottersen et al. 2001). A response may not be readily apparent because of the ability of the system to resist change in proportion to its intrinsic buffering capability. Reactions may take years or even decades to progress if the rate of change is slow or if the response of the system operates on a time lag (Rapport et al. 1998). Time lags are caused by indirect links between components; the effects are temporarily stored in compartments before propagating throughout the system (Jørgensen 2002, Fath 2004). Indirect links often act to change the interaction type to a more

favourable one depending on the organisms involved. Links result in both weak and strong interactions among system components, but the distribution is skewed toward weak interactions that act to dampen oscillations within the system (McCann et al. 1998, Wootton 2002, Emmerson and Yearsley 2004). Change can appear to affect the entire system or parts of it differently and significantly because the relationships between ecosystem processes and the patterns created by these processes also alter with spatial-temporal scale. Ecosystems that are large relative to the influence of the perturbation tend to maintain a relatively constant structure for a longer time (Jørgensen 2002). When a response eventually occurs, it is difficult to determine the forcing factor (Collie et al. 2004). This problem has been reported for the North Sea (Clark and Frid 2001), the Pacific Ocean (McFarlane and Beamish 2001, Beamish and Mahnken 2001, Bertrand et al. 2004), and other regions (Spencer and Collie 1997, Nystrom et al. 2000, Fréon et al. 2003, Sharp 2003, Yndestad 2004).

Change can result from natural or anthropogenic external causes or from internally generated fluctuations, such as those inherent in the system's predator-prey cycles (Scheffer and Carpenter 2003). Organisms and biological processes are usually tuned to annually repeating changes, such as seasonal events like spring blooms or winter ice cover. Species with r-selected life-history strategies have evolved a reproductive strategy to take advantage of randomly fluctuating environments (Bakun 1986, Cury et al. 2000, Jørgensen 2002). Episodic disturbances are usually incorporated into ecosystem behaviour unless species loss occurs to such an extent that the system undergoes structural and functional transformation (Turner et al. 2003). At small spatial scales, change may appear to be devastating; whereas at large scales, change often is a natural,

integral and expected dynamic of the ecosystem. In highly productive regions, for example, pelagic sardines (the genera *Sardinops* and *Sardina*) have evolved a reproductive strategy (exploit a "loophole") to cope with the El Niño Southern Oscillation (ENSO) cycle, a natural but irregular phenomenon that can have devastating effects on local biological components of upwelling systems (Bakun and Broad 2003). The loophole exists because an El Niño is bad for all, but reduced predation on larvae and juveniles results in the production of a strong sardine year class.

The relationship between biological processes and atmosphere/ocean physics varies with different temporal scales (Francis et al. 1998). Small pelagic fish populations may appear to be devastated by climatic factors in the short-term, but reconstruction of long-term records indicates otherwise. Sediment core analysis of fish scale deposits to obtain relative abundances of sardine and anchovy, in concert with ice core and tree ring data that provide temperature data over the past 1400–1700 years have shown that sardine-anchovy cycles are natural events (Klyashtorin 2001). Dominant, out-of-phase fluctuations of each species occur approximately every 60 years and are closely linked to climatic changes that operate on long cycles. Finney et al. (2002) used sediment cores from Pacific salmon nursery lakes over 2200 years to show that salmon population fluctuations alternate in and out of phase with sardine and anchovy populations for most of that time period, indicating that these populations may also exhibit cyclic behavior. Studies of sediments and ice core rings over the past 210,000 years have found deep-sea benthic organisms also show cyclic patterns closely linked to deep- and surface-water oceanographic variability (Cronin et al. 1999). Analysis of diatom and cladoceran deposits, catch records, and sedimentary $\delta^{15}N$ in the North Pacific have shown that

environmental variability occurs on interannual, decadal and centennial scales, as does its effect on ecosystem productivity and trophic interactions (Spencer and Collie 1997, Finney et al. 2000, Finney et al. 2002, Fréon et al. 2003). Although ecosystems appear to be capable of withstanding natural cycles and variations, disruption occurs when strong anomalies appear.

Human-induced changes rescale spatial and temporal patterns of landscapes and system dynamics and alter the scales at which natural disturbances occur, affecting how an ecosystem responds to and recovers from perturbations (Urban et al. 1987, Nyström et al. 2000). For example, overfishing clearly accelerates the frequency of natural cycles of periodicity in pelagic fishes, with repercussions at all trophic levels (Steele and Henderson 1984). Fishing also affects long-term cycles by dampening and shortening peaks during periods of high abundance and deepening and lengthening troughs during periods of low abundance (Cury et al. 2000); fluctuations are amplified by a fishing-induced lack of large, old fish with high reproductive capabilities (Pauly and Maclean 2003). Human-induced changes tend to occur with greater frequency, leaving systems little time to adapt, or with longer duration than natural events so that systems so perturbed are under a continual stress (Nyström et al. 2000). Some effects of human disturbance are less obvious than others, or the resultant changes occur at such a slow rate that they may not be easily discernable (Scheffer and Carpenter 2003). Change, whether natural or man-made, can have adverse effects on stability by destroying ecosystem complexity and therefore ecosystem connectedness, structure and function (Urban et al. 1987, Cury et al. 2000, Loreau 2000).

1.2. Impact of fishing on natural populations

With a marine catch of approximately 85 million metric tons in 2002 (FAO 2004) and with approximately half the global fish stocks fully exploited (Botsford et al. 1997) and 25% overexploited (FAO 2004), fishing invariably has an impact on populations, communities and large marine ecosystems throughout the world. The effects of fishing often take many years to decades to become manifest due to the longevity of the species harvested. Overfishing weakens the ecosystem, increasing vulnerability to the effects of other factors or to what would otherwise have been minor perturbations (Pauly and Maclean 2003). Declines in one species can precipitate complete and total ecosystem change. Some of the better known examples include the removal of predators and competitors by exploitation that resulted in unchecked population growth of sea urchins that subsequently overgraze kelp forests (Jackson et al. 2001) and overfishing of herbivorous fishes in coral reef systems that resulted in macroalgae overgrowth when sea urchins, another herbivore, declined due to disease (Nyström et al. 2000).

The effects of fishing on individuals, populations and communities are well known and have been described in great detail (e.g. Botsford et al. 1997, Bianchi et al. 2000, Cury et al. 2000, Koslow et al. 2000, Law 2000, Stevens et al. 2000, Zwanenburg 2000, Jackson 2001, Rosenberg 2003b, Hutchings 2004). Some suspected effects are lesser known, such as genetic and structural population changes that result from selective pressure (Cury et al. 2000, Olsen et al. 2004), loss of genetic diversity (Jennings and Kaiser 1998), and changing genetic composition (Gislason et al. 2000). Because evolutionary response to exploitation is much slower in comparison to phenotypic

responses, evolutionary responses are often overlooked in fisheries assessments, which are concerned primarily with short-term population forecasts. Other indirect effects are much harder to determine and are often postulated in response to changes in trophic and community dynamics (Gomes and Haedrich 1992, Botsford et al. 1997, Jennings and Kaiser 1998), removal of top predators (Frank et al. 2005, Myers et al. 2007), and loss of critical habitat (Agardy 2000). Responses include intense competition between fishers and large mammals or other large predators for the remaining prey (Pauly and Maclean 2003), replacement of depleted target species with others that occupy similar ecological niches or roles (Fogarty and Murawski 1998), and expanding populations of species, such as seabirds and seals, that previously competed with top fish predators (Frank et al. 2005). It is very difficult to determine if indirect responses are a result of overexploitation, other anthropogenic influences, or natural environmental fluctuations (Gislason et al. 2000)

1.3. Regime shifts

The behavior of many systems, including fishery ecosystems, is characterized by sudden episodic changes (otherwise known as abrupt fluctuations, regime shifts or "surprises"), which are regarded as jumps between alternative states brought about by natural environmental changes or, more recently, human induced changes (Steele and Henderson 1984, Caddy 1996, Augustine et al. 1998, Cury et al. 2000, Fath et al. 2003). Examples of these "surprises" are the abrupt desertification of the Saharan region (deMenocal et al. 2000), collapse of coral reef systems (Nyström et al. 2000) and shifts in fish stocks (Steele and Henderson 1984, Mittelbach et al. 2006). The forcing factor does not have to be large to trigger an ecosystem shift and there are often no warning signals

that a shift is about to happen (Scheffer et al. 2001). Shifts may be a necessary part of ecosystem function (Turner and Johnson 2001) and, in some cases, may act as a way for systems to eliminate weak components, e.g. the widespread extinctions in archaic marine fish species following a global cooling period in the late Devonian (McGhee 1996). Transitional stages, where systems are moving from one state to another, can be long relative to the life cycles of the species involved (Steele and Henderson 1984). But the actual shift is usually abrupt, brought about by a combination of internal processes and external forcing factors, and no warning signs are apparent beforehand (Scheffer et al. 2001, Scheffer and Carpenter 2003). A shift, or flip, occurs over a short time span, often years, whereas a regime, the stable period, operates on a decadal scale (Sherman 1990).

In marine systems, regime shifts are considered to be low-frequency, high-amplitude changes in oceanic and atmospheric conditions that cause changes to occur in biological components of ecosystems. Changes must be seen in several trophic levels and are most rapid at the highest trophic levels, they must trigger abrupt changes in species abundances, community composition, and trophic organization, and they must occur on a regional scale in order to be termed a regime shift (Francis et al. 1998, McGowan et al. 1998, Hare and Mantua 2000, McKinnell et al. 2001, Collie et al. 2004). The actual trigger (forcing factor) of a particular regime shift is often poorly understood; however, the general belief is that atmospheric patterns and oceanic circulation play a major role (Ebbesmeyer et al. 1991). Regime shifts were used in the past to describe sardine-anchovy cycles (Lluch-Belda et al. 1989), but now the term is more commonly used to describe abrupt changes in important commercial fish stocks in conjunction with oceanographic and climatic changes (Anderson and Piatt 1999, Beamish et al. 1999, Hare

and Mantua 2000, Beamish et al. 2004). Fish stocks are used as a defining biological factor because fish are typically the longest-lived component in marine/freshwater ecosystems and, therefore, the species showing the longest temporal scale of change (longest trend). The notion of regime shifts is not new. The Russell cycle, first described in the 1960s by Sir Fredrick Russell, was a striking change in community structure in the English Channel involving all trophic levels (Cushing and Dickson 1976). Recently, there has been great interest in determining the relationship between fishing and other human activities to regime shifts, primarily with respect to fisheries management.

Time series data are one method to look for evidence of regime shifts. Physical-chemical-biological components are highly variable on yearly or decadal scales; trends become most apparent with long-term data. Explicit consideration of time lags is important for identifying regime shifts as biological components often tend to react at different scales than do physical components (Francis et al. 1998, Beaugrand 2004).

Unfortunately, long time series of biological data are quite rare in marine systems unless one uses non-traditional data sources, such as fossil or scale records from zooarchaeological sources. Research survey programs, which collect fisheries independent data, have been operating in many countries for less than 50 years, although there are a few notable exceptions (Cushing and Dickson 1976, Ravier and Fromentin 2001, Ravier and Fromentin 2004). Landings data are often used as a proxy of fish abundance due to the length of their time series; they provide a rough estimation of the scale of the resource based on what was removed. Landings data, on their own, have limited use as an index of abundance because they also tend to reflect trends in economics, fishing effort, and management regulations (Taggart et al. 1994). Another

type of fisheries-dependent relative abundance index is catch-per-unit-effort (CPUE), or catch rate; an assumption is that at small spatial scales, catch rate is proportional to the product of fishing effort and density (Maunder and Punt 2004). Changes to effort, such as temporal and spatial changes, will affect catch rate (Hilborn and Walters 1992). Any changes to the management of a species will affect CPUE by changing fishing behaviour and fishing statistics (Sampson 1991, Campbell 2004). If the CPUE index is standardized correctly by adjusting (removing) the effect of factors that may influence the index other than abundance, such as vessel characteristics, it may be a useful index of relative abundance (Maunder and Punt 2004). However, there are a few cases where CPUE indices have appeared to increase as the stock collapsed (hyperstability, Cooke and Beddington 1984, Rose and Kulka 1999) or hyperdepletion may occur (Prince and Hilborn 1998).

Many traditional methods have been used to analyze fisheries time series, but have met with varying success (e.g., Fogarty 1989; Stergiou 1989, 1991; Pajuelo and Lorenzo 1995; Stergiou and Christou 1996; Stergiou et al. 1997; Park 1998; Lloret et al. 2001; Pierce and Boyle 2003; Georgakarakos et al. 2002; Mantua 2004) because they often do not incorporate explanatory variables and often use single, not multiple time series.

1.4. Thesis outline

Different scales of change imply the need for different approaches to study change in ecosystems (Steele 1998); these are typically spatial or temporal scales. I will determine if proximate causes for ecosystem change might be apparent at different biological and spatial scales by analyzing time series at fairly short temporal scales (< 30 years). In

Chapter 2, I describe in detail the time series methodology I use: min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA). In Chapter 3, I determine if trends can be ascertained using these methods for *Sebastes spp.*, where population units are well defined, cover a fairly small spatial scale, and abundance has been estimated by the Department of Fisheries and Oceans, and look for factors that may explain the estimated trends. In Chapter 4, I look at more problematic species. These are deep-sea species with broad geographic ranges, on the scale of ocean basins. I determine if trends in relative abundance exist using generalized linear models. Many questions arose from this analysis, including a "Brief Arising" sent to Nature by the Department of Fisheries and Oceans, some of which are dealt with in Chapter 5. In Chapter 6, I investigate if the data are adequate to describe the trends observed; is the loss of data incurred by using statistical rigor biasing results? I use data for two of the deep-sea species, *Coryphaenoides rupestris* and *Macrourus berglax*, and explore possible causal factors for observed trends in their populations. In Chapter 7, I determine if trends in abundance and mean size of the shelf and slope demersal fish community in NAFO Divisions 2J3KL can be determined using MAFA and DFA. Do these approaches show any surprising results when combining data from species with very different life history characteristics? I summarize my main findings in Chapter 8. The main chapters (3–7) were written as separate manuscripts, necessitating a brief repetition of methodologies.

Chapter 2. As Time Goes By: A Few Methods for Analyzing Time Series

"All models are wrong, but some are useful." – George Box
"A model is a lie that helps us to see the truth." – Robert MacArther

Analyses of trends in ecosystem patterns and processes are important for understanding the spatial and temporal dynamics of the system (Jensen et al. 1996). Analyses of spatial gradients are useful for studying components that have the potential to shape ecosystem structure (Clarke and Ainsworth 1993). For example, multi-dimensional scaling has been used to assess meiofaunal community responses to pollution gradients at an offshore drilling site (Gee et al. 1992), the response of macrobenthos to pollution and disturbance gradients at an offshore drilling site in the North Sea (Warwick et al. 1990), and the response of diatoms to nutrient loading gradients in a lagoon (Clarke and Ainsworth 1993). Analyses of temporal trends allow for an understanding of the system dynamics and the potential limits of system dynamics (Jensen et al. 2001); studies can be conducted over many spatial scales. Time series methods used to look for discontinuities include regime shift analysis and chronological clustering, while regression, correlograms, ARIMAX (auto-regressive integrated moving average models with exogenous variables), spectral analysis, DFA (dynamic factor analysis) and MAFA (min/max autocorrelation factor analysis) are used to identify trends and patterns,

Regime shift analysis (RSA) requires time series data be divided into two or more regimes *a priori*; this type of analysis is useful if one has reason to look for the effects of a sudden change at a particular time (Ebbesmeyer et al. 1991). RSA was used to determine if evidence existed for regime shifts in the northern Pacific Ocean in 1977 and

1989 (Hare and Mantua 2000). McFarlane et al. (2000) also used RSA to document shifts in recruitment of seven fish species over the same region and time period. In addition to looking for steps, which are indicative of a change, changes in averages over the regime can also be compared (Zuur et al. 2007). Rudnick and Davis (2003), however, have shown that this type of analysis will always indicate a stepwise shift, especially when numerous short time series are amalgamated. They fabricated time series to prove that shifts are typical of red noise, or low frequency noise inherent in every system.

Chronological clustering, another type of analysis that looks for abrupt changes, was originally designed to study successional changes in ecosystems as succession tends to proceed in abrupt steps rather than smoothly (Legendre et al. 1985). Bell and Legendre (1987) used chronological clustering to test for discontinuities in the chronological distribution of morphological types of fossil sticklebacks *Gasterosteus doryssus* over time. This method can also test for abrupt shifts in ecosystems. Using the data from Hare and Mantua (2000), Zuur et al. (2007) found that chronological clustering identified the same two major shifts in 1977 and 1989 found using RSA. Chronological clustering differs from RSA because it can test whether the ecosystem has reverted to its original state, although there is much debate over whether large, open ecosystems are capable of reverting (Scheffer et al. 2001, Scheffer and Carpenter 2003).

Most methods of traditional time series analysis, such as spectral analysis or ARIMA (sometimes referred to as Box-Jenkins models), cannot handle missing values and require the series to be stationary; this involves removing the trend from the series (Ljung 1987, Legendre and Legendre 1998). Spectral analysis is typically used to look for periodicities in time series (Platt and Denman 1975, Priestley 1981), while ARIMA is primarily used

for forecasting (Chatfield 1989). These traditional methods have been applied to fisheries time series with varying success (e.g., Fogarty 1989, Stergiou 1989, 1991, Pajuelo and Lorenzo 1995, Stergiou and Christou 1996, Stergiou et al. 1997, Park 1998, Lloret et al. 2001, Pierce and Boyle 2003, Georgakarakos et al. 2002, Mantua 2004). Additional methods, such as split moving-window boundary analysis, locally-weighted regression (or *loess*), generalized additive models, and generalized linear models are often used to analyze fisheries time series data (e.g., Daskalov 1999, Walsh and Kleiber 2001, Daskalov 2003, Beaugrand 2004, Sacau et al. 2005, Unwin et al. 2005); however, these techniques typically do not estimate multiple trends within the same dataset. Standard multivariate techniques, such as principal component analysis, are not appropriate for longer time series because they cannot retain the time order of the data (Chatfield 1989, Solow 1994).

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) are multivariate methods designed specifically for shorter time series (at least 15-25 years) and are not burdened by the shortcomings listed above (Zuur et al. 2007). These techniques assume that the system is changing gradually over time. Stochastic trends are allowed in these models, i.e. trends are not restricted to straight line or strict cosine functions (Zuur et al. 2007). Furthermore, the effects of time lags in the explanatory variables can be explicitly evaluated (Zuur et al. 2003a, Zuur and Pierce 2004). In the past, these techniques have been used primarily in economics and psychology (e.g., Molenaar 1985, 1989, 1993, Molenaar and de Gooijer 1988, Harvey 1989, Lütkepohl 1991, Molenaar et al. 1992, 1999). More recently, they have been applied to oceanographic data (Mendelssohn and Schwing 2002).

Applications of MAFA and DFA to fisheries data are few, but the numbers are growing. Solow (1994) used MAFA to estimate trends in Georges Bank fishes and Gulf of Maine zooplankton. MAFA has also been used in analysis of spatial structuring of demersal fishes in the Gulf of Lyons (Gaertner et al. 1999), to explore the effects of prey abundance and environmental changes on marine mammal populations (CIESM 2004), and to explore the effect of increased aquaculture on fisheries landings in oligotrophic seas (Machias et al. 2006). Erzini (2005) and Erzini et al. (2007) used both MAFA and DFA to analyze trends and relationships with external factors in Portuguese fisheries landings. DFA has also been used to model trends in Norwegian lobster *Nephrops norvegicus* from fishing grounds in northern European waters (Zuur et al. 2003b), biomass trends in Wadden Sea benthic macrofauna (Zuur et al. 2003a), and trends in Atlantic squid *Loligo forbesi* (Zuur and Pierce 2004). MAFA and DFA have also been used to analyze trends in demersal species (Devine et al. 2007) and deep-sea species (Devine and Haedrich (in press)) from research survey data from the Northwest Atlantic and demersal species from the Northeast Atlantic (Erzini et al. 2005).

2.2. Min/max autocorrelation factor analysis: MAFA

MAFA, a type of principle component analysis for time series, can extract trends, estimate index functions that represent the common behavior for the original time series, and smooth data (Switzer and Green 1984, Shapiro and Switzer 1989, Solow 1994, Zuur et al. 2007). MAFA, unlike traditional PCA, retains the time order of the data. MAFA constructs a set of orthogonal linear combinations of the original time series with smoothness, as measured by lag-one autocorrelation, decreasing from the maximum

Min/max autocorrelation factor analysis isolates the highly autocorrelated series (maximum autocorrelations), which are the trends, from the weakly autocorrelated series (minimum autocorrelations), which are the noise components (Shapiro and Switzer 1989). Trends are referred to as MAFs (maximum autocorrelation factors).

2.2.1. Using MAFA to extract trends

Let $X_i(t)$ denote the value of the i^{th} response time series at time t, where $i = 1, 2, \ldots, p$ and $t = 1, 2, \ldots, n$. The vector of input data is

$$\mathbf{X}(t) = (\mathbf{X}_1(t), \ldots, \mathbf{X}_p(t))'$$

MAFA calculations are on centered **X** data, such that $\sum_t X_i(t) = 0$ for each i. The output MAF series (trends) are similarly constructed:

$$\mathbf{Y}(t) = (\mathbf{Y}_1(t), \ldots, \mathbf{Y}_p(t))'$$

where $i = 1, 2, \ldots, p$ and $t = 1, 2, \ldots, n$.

A set of orthogonal linear combinations of the original time series (MAFs) are constructed:

$$\boldsymbol{Y(t)} = \boldsymbol{X(t)} \times \boldsymbol{A}$$

where **Y** is an $n \times p$ matrix containing the MAFs, **X** is an $n \times p$ matrix containing the original time series, and **A** is a $p \times p$ matrix not dependent on time (Shapiro and Switzer 1989); **A** contains the factor loadings (Zuur et al. 2007). MAFA can be thought of as a scaled principal components analysis, followed by a first-differencing on the principal components, and then a second principal component analysis of the first differences (Shapiro and Switzer 1989). Linear rescaling of inputs or other linear transformations will have no effect on the MAF outputs (Shapiro and Switzer 1989).

The first MAF has the form:

$$Y_1(t) = \boldsymbol{A}' \boldsymbol{X}(t)$$

where $\boldsymbol{X}$ is the $n \times p$ matrix composed of the original time series and $\boldsymbol{A}$ is a $p \times p$ matrix (a weight factor). The covariance matrices of the original time series are

$$\mathbf{C} = (\mathbf{X}'\mathbf{X})/n$$

and the first differences are

$$\mathbf{V} = (\mathbf{D}'\mathbf{D})/(n-1)$$

where $\boldsymbol{D}$ is the $(n-1) \times p$ matrix composed of the first differences in the original time series. Since

$$(\mathbf{A}'\mathbf{V}\mathbf{A})/(\mathbf{A}'\mathbf{C}\mathbf{A}) = 2(1-r_1)$$

where r_1 is the lag 1 autocorrelation of $Y_1(t)$, then to maximize the lag-one autocorrelation, the weight vector $\boldsymbol{A}$ should be proportional to the eigenvector of the matrix $\mathbf{C}^{-1}\mathbf{V}$ corresponding to the smallest eigenvector of $\mathbf{C}^{-1}\mathbf{V}$ (which is equal to $2(1-r_1)$).

MAFA axes are mutually uncorrelated with unit variance and MAFs have decreasing autocorrelation at lag 1 (Zuur et al. 2007). Typically, only the first few MAFs show significant autocorrelation. In PCA, the first axis explains most of the variance; in MAFA, the first axis represents the highest autocorrelation at lag 1 and is therefore the main trend underlying the data. Other axes represent less important trends.

To determine how many axes to use, a randomization process can be used to obtain p-values (Solow 1994). The first MAF is extracted, its lag 1 autocorrelation is determined,

and its significance is tested against ordered lag 1 autocorrelations found by randomization. If the first MAF is not significant, the process terminates; no p-value is generated if the autocorrelation is not significant. If it is significant, the process continues with the second MAF. The process ends when an axis is determined to be not significant.

2.2.2. MAFA as a smoothing function

Using the MAFA technique to re-express time series as weakly and strongly autocorrelated series allows for smoothing in the absence of external models of noise, i.e. trend information is combined in the highly autocorrelated series, which act to amplify the information, while weakly autocorrelated series collect the high frequency or noise components of the original series (Shapiro and Switzer 1989). The approach uses an adaptive smoother (Friedman 1984) that varies the bandwidth depending on the amount of autocorrelation, the most weakly autocorrelated output series virtually disappear with this type of smoothing (Shapiro and Switzer 1989).

As defined previously (section 2.1)

$$\boldsymbol{Y}(t) = \boldsymbol{X}(t) \times \boldsymbol{A}.$$

Let $Y_i^*(t)$, $i = 1, 2, \ldots, p$ denote the differentially-smoothed version of the MAF output time series $\boldsymbol{Y}_i(t)$. The smoothed version of the original time series is defined as

$$\mathbf{X}^*(t) = \mathbf{A}^{-1}\mathbf{Y}^*(t).$$

This approach combines information from all time series to smooth each of them, does not require modelling of the series, makes no assumptions regarding the residuals or noise, and introduces less smoothing-induced bias by simultaneously smoothing both the structural and noise components of the series (Shapiro and Switzer 1989).

2.2.3. Using MAFA to estimate index functions

The first MAF represents an index series that best tracks the common behavior of the original time series. If the time series show strong autocorrelation, yet are mutually uncorrelated, a single index series will not capture all the essential time variation in the original series (Shapiro and Switzer 1989). MAFA is non-parametric and searches for a local smoothness by maximizing the local autocorrelation. This maximization method should be effective in determining a variety of trend shapes and is not restricted solely to, for example, linear trends (Shapiro and Switzer 1989).

2.2.4. MAFA Implementation

Factor loadings determine relationships between the original response time series and a particular MAFA axis (Zuur et al. 2007). Canonical correlations, or cross-correlations, between MAFA axes and the original response time series determine which time series are related to a particular trend. Cross-correlations between the MAFA axes and explanatory variables are estimated to determine if there are significant relationships between the MAFA trends and explanatory variables. MAFA was completed using the software package Brodgar (http://www.brodgar.com).

2.3. Dynamic factor analysis: DFA

DFA is a technique for modelling short, non-stationary time series in terms of common trends and explanatory variables (Zuur et al. 2003a,b, Zuur and Pierce 2004). DFA can determine common patterns in time series, evaluate interactions between response variables, and determine the effects of explanatory variables (Zuur et al. 2003a). DFA is a

dimension-reducing technique that models N time series in terms of M common trends, where M is less than N. DFA is similar to other dimension reduction techniques in that the axes are restricted to smoothing functions over time; however, DFA differs in that it assumes trends correlate over time (Zuur et al. 2003a). Dynamic factor analysis does not require pre-selection of data and therefore provides an objective assessment of common trends and relationships of response time series with explanatory variables. The DFA models discussed below are based on normality assumptions.

2.3.1. The inner workings of DFA

To illustrate DFA, univariate models are first modeled with no explanatory variables

$$y_t = \alpha_t + \varepsilon_t$$

where y_t is the response series measured at time t, where $t = 1, 2,\ldots,T$ and α_t is the unknown trend at time t

$$\alpha_t = \alpha_{t-1} + \eta_t .$$

This relationship is also termed a random walk trend plus noise model (Harvey 1989) and can also be written as:

Trend at time t = trend at time t-1 + noise at time t.

DFA models time series as a linear combination of common trends, explanatory variables, a constant level parameter and a noise component; the constant level parameter is the intercept term in a regression model (Zuur et al. 2003a). DFA begins with a simple model that contains only M common trends and noise:

$$y_{it} = z_{i1}\alpha_{1t} + z_{i2}\alpha_{2t} + \ldots + z_{iM}\alpha_{Mt} + e_{it}$$

where y_{it} represents the value of the *i*th time series at time *t*, α_{jt} is the *j*th common trend, z_{ij} is the factor loading and e_{it} is noise (Zuur et al. 2003a). This model is written in matrix notation as:

$$\mathbf{y}_t = \mathbf{Z}\boldsymbol{\alpha}_t + \mathbf{e}_t$$

where $\mathbf{y}_t$ is a $N \times 1$ vector containing the values of the N time series at time t, $\boldsymbol{\alpha}_t$ is a vector of dimension M, containing the values of the M common trends at time t, $\mathbf{e}_t$ is an $N \times 1$ matrix of error terms, assumed to be normally distributed (mean=0 and covariance matrix **R**), and **Z** is a $N \times M$ matrix containing the factor loadings. Factor loadings determine which trends are important to a response series and which group of response series are related to a common trend (Zuur et al. 2003b). **Z** determines the exact form of the linear combinations of the common trends.

The trends, which represent underlying common patterns over time, are modelled as:

$$\boldsymbol{\alpha}_t = \boldsymbol{\alpha}_{t-1} + \mathbf{f}_t$$

where $\mathbf{f}_t \sim N(0, \mathbf{Q})$ and $\mathbf{f}_t$ is independent of $\mathbf{e}_t$, but the normality assumption is not strictly necessary (Zuur et al. 2003a). **Q** is a diagonal covariance matrix. The corresponding diagonal element of **Q** determines the amount of smoothing. If the corresponding diagonal element of **Q** is relatively small, the contribution of the error component is also likely to be small for all *t*, and the trend is a smooth curve. If **Q** is large, more variation is shown and the trends are independent smoothing functions. The covariance matrix **Q** can be converted to a correlation matrix and the major diagonal becomes the identity matrix, therefore $\mathbf{Q} = \mathbf{I}$; this allows for the estimation of **Q** without having to use the EM algorithm (not a trivial process, outlined in Zuur et al. 2003a). A further advantage of

setting **Q** equal to the identity matrix is that a unique solution exists for the factor loadings (Zuur et al. 2003a). Once the parameters have been estimated, a factor rotation, such as varimax rotation, can be applied to the estimated factor loadings and trends. Applying the varimax rotation attempts to relate each time series to just one of the common trends (Basilevsky 1994).

The covariance matrix of the response variables is given by

$$\text{Cov}(\mathbf{y}_t) = \mathbf{Z}\mathbf{Z}^t + \mathbf{R}.$$

The major diagonal of **R** is **I**, the identity matrix, as defined above. The covariance matrix **R** is modelled as either a diagonal matrix or a symmetric positive-definite matrix. The use of a diagonal matrix has advantages for interpretation and diagnostic tools, but it can lead to common trends that are only related to two or three response variables. In a symmetric positive-definite matrix **R**, off-diagonal elements of **R** represent information in two response variables that cannot be explained by the common trends. The disadvantage of a symmetric positive-definite covariance matrix is that the number of parameters estimated increases considerably (Zuur et al. 2003b). Complex models, or those with a greater number of parameters, tend to be more sensitive to changes to their parameters. The general rule is to choose the simplest model with the fewest parameters, unless statistical tests show it is not the "best" model.

The covariance matrix **R** is inspected to find a pattern in the joint interaction of response variables that cannot be explained by the common trends (Zuur et al. 2003a). If the number of elements is large, visual inspection is unrealistic. The covariance matrix **R** can be transformed using multidimensional scaling (MDS). **R** is transformed into a dissimilarity matrix using

$$d(y_1, y_2) = \left| \sqrt{2(1 - corr(y_1, y_2))} \right|$$

where $d(y_1,y_2)$ represents the dissimilarity between y_1 and y_2 and absolute values of the correlation, necessary because large negative correlations that would otherwise by considered dissimilar, are used (Krzanowski 1988, Zuur et al. 2003b). Points close to each other after MDS have high absolute correlation and share information not explained by the common trends and explanatory variables.

Explanatory variables are included and modelled as in linear regression

$$\mathbf{y}_t = \mathbf{Z}\boldsymbol{\alpha}_t + \mathbf{c} + \mathbf{D}\mathbf{x}_t + \mathbf{e}_t$$

where $\mathbf{x}_t$ is the $K \times 1$ matrix containing the K explanatory variables at time t, $\mathbf{c}$ is a constant level parameter of dimension $N \times 1$ that allows each linear combination of trends to move up and down (i.e., functions as the intercept in regression), and $\mathbf{D}$ is an $N \times K$ matrix containing the regression parameters. Here, $\mathbf{x}_t$ represents real variables while $\boldsymbol{\alpha}_t$ represents hypothetical variables; $\boldsymbol{\alpha}_t$ is the information shared by the response variables that cannot be explained by the measured explanatory variable(s) (Zuur et al. 2003a). A model with no latent variables (variables not measured but which may explain trends) but only explanatory variables makes interpretation easier (Zuur et al. 2003b).

The underlying statistics are explained in more detail in Zuur et al. (2003a,b).

2.3.2. Selection criteria

The number of common trends modelled should ideally be less than the number of time series used and preferably as small as possible without sacrificing goodness of fit. The larger the number of common trends used, the better the model fit but the greater the

number of parameters that must be estimated. Akaike's Information Criterion (AIC) was used initially to determine the optimal model in terms of goodness of fit and the number of parameters. The AIC is given by

$$AIC = -2Ln(s_m^2) + 2m,$$

where m is the number of parameters in the model and s_m^2 is the average squared residual (or log likelihood function) for the model. The model with the smallest AIC value was selected as the best model that reflects the tradeoff between the fit of the model (log likelihood function) and the model's complexity (number of parameters) (Sakamoto et al. 1986). The AIC, although criticized because it has a tendency to select too many autoregressive terms in autoregressive models, was used here because the dynamic factor model does not contain autoregressive terms (Zuur et al. 2003b). Other model validation tools, such as standard regression diagnostics, can then also be used to determine the goodness of fit in DFA.

2.3.3. DFA Execution

DFA was implemented using the software package Brodgar (http://www.brodgar.com) and a custom program written by A. Zuur specifically for my data. I needed a specialized program because of the number of models I ran (e.g., 15,162 models for Chapter 7); my explanatory variables included time lags up to 18 years for each variable. Models with lagged variables indicate that the effects of the common trend occur with a time delay.

All time series were standardized to a mean of zero and a standard deviation of one, required for the interpretation of the factor loadings. If the time series are on different scales, factor loadings may only reflect differences in the scale of the series instead of real

interactions between the series (Zuur et al. 2003a). Factor loadings determine the importance of a particular trend. Loadings also represent common patterns over time for a specific response variable and/or different groups of response variables (Zuur et al. 2003a).

Canonical correlations, cross-correlation between response variables, and the estimated common trends can be used instead of factor loadings to detect the relationship between response variables and trends (Zuur et al. 2003b). An advantage of this method is that canonical correlations can be estimated for series with missing values; factor loading cannot.

DFA can be viewed as a regression model and is therefore subject to the same underlying assumptions: normality, non-homogeneity of residuals, and independence. Non-normality and non-homogeneous residuals can be addressed by transforming the data. I have had to transform most of my response time series to meet these assumptions. DFA cannot handle count data, and the normality assumption is difficult to meet with count data. The models have not been modified to include Poisson or negative binomial distributions at this time. Violating the normality assumption, however, is not a major violation; violating the independence assumption is the most serious error. Neither this assumption, nor non-homogeneous residuals, were violated in the following chapters.

All data used in the time series were relative abundance indices (CPUE indices from fishery independent research surveys), not count data. Chapter 3 included stratified estimates of abundance, estimated from research survey data using DFO stratified analysis STRAP software (Smith and Somerton 1981), while Chapters 4–7 use estimates of stratified number per standardized research survey tow (a type of CPUE index).

Here I have described the inner workings of MAFA and DFA. In the next chapter, I begin with a simple illustration of their use. I explore dynamics of six separate and well-defined populations of *Sebastes spp.* in the Northwest Atlantic, determine if these dynamics are related to one or more external factors, and if populations respond to these factors on a time lag.

[2]Chapter 3. Once in a While: Redfish Populations in the Northwest Atlantic Ocean Affected Differently by Environment and Exploitation Operating on Different Temporal Scales

> There was also growing anxiety about the destruction wrought by shrimp dragging on other species such as redfish, flounder and cod. This was because the small mesh size needed to catch shrimp could also catch large quantities of juvenile members of these species. Reports of "the ocean turned red" during the shrimp fishery by the huge amounts of dead baby redfish discarded from shrimp nets had circulated since the 1970s...seemed no concern to the fishers, who appeared to take this sight for granted.
>
> – C.T. Palmer and P. Sinclair (1997)

The fishery ecosystem on the Newfoundland and Labrador Shelf supported one of the world's greatest fisheries. Redfish *Sebastes spp.* have been fished on both sides of the Atlantic since the 1950s in the longest running deepwater fisheries (Koslow et al. 2000). The redfish fishery in the Northwest Atlantic peaked in the late 1950s at almost 400,000 tons (Koslow et al. 2000). Recently, many stocks have been decimated and some groundfish fisheries, including Atlantic cod *Gadus morhua,* have been under moratorium since the mid-1990s. As cod catches were declining, fishing effort was again redirected towards redfish, subsequently resulting in declines in their populations (Hamilton et al. 2004). The declines have resulted in the closure of the Gulf of St. Lawrence, northern and eastern Grand Bank, and Labrador Shelf redfish fisheries, while quotas have been reduced for the Laurentian Channel stocks (Morin et al. 2004). The closure of the fishery afforded some protection for redfish populations, but many juveniles are still captured as by-catch in the shrimp fishery or experience high natural mortality as a result of natural predation

[2]This chapter was submitted as a technical report in partial fulfillment of a contract with WWF-Canada. Paper is in preparation for journal submission, under the title: Temporal trends in redfish *Sebastes spp.* abundance in the Northwest Atlantic: the relative importance of fisheries and environment.

and poor environmental conditions (Morin et al. 2004). Although some redfish stocks declined, others with more southern ranges remained stable or increased in biomass (Branton 1999, Mayo et al. 2002). The dynamics displayed by different redfish populations and their potential causes have not been rigorously investigated.

Three species of redfish are found in the northwest Atlantic: the deepwater redfish, *Sebastes mentella* Travin, the Acadian redfish, *S. fasciatus* Storer, and the golden redfish, *S. marinus* Linnaeus. *S. mentella* and *S. fasciatus* dominate Canadian catches. *S. marinus* is found mainly in waters near the Flemish Cap and Newfoundland's northern and Grand Banks (Scott and Scott 1988). *S. mentella* is typically found at temperatures ranging from 3–8° Celsius and at depths of 350–700 meters, although it has been captured as deep as 1100 m (Scott and Scott 1988). *S. fasciatus* is a Northwest Atlantic endemic found typically at depths between 128–366 meters, although it has been captured at depths to 592 m (Kelly and Barker 1961). Temperature preference is 2.8–8.3 °C (Kelly et al. 1972). *S. marinus* prefers a temperature range of 3–7 °C and is found at depths between 100–1000 m (Froese and Pauly 2006), but is considered to prefer depths intermediate to the other two *Sebastes* (Scott and Scott 1988).

All redfish display life-history characteristics that are typical of many deep-sea fishes; they are long-lived, slow growing, late maturing and exhibit low fecundity (Koslow 1996). Maximum age for the three *Sebastes spp.* range from 45 years for *S. fasciatus* (Laurel 2004) to 60–75 years for *S. mentella* and *S. marinus* (Campana et al. 1990, Froese and Pauly 2006). Average age at 50% maturity for most populations of *Sebastes fasciatus* in Canadian waters of the Atlantic Ocean is 9.4 years, 10-12 years for *S. marinus*, and 10-

13 years for *S. mentella* (Froese and Pauly 2006). Growth, expressed as the Brody growth coefficient ranges from 0.05–0.19 for *Sebastes spp.* (Saborido-Rey et al. 2004, Froese and Pauly 2006).

Redfish are known to perform diel vertical migrations, rising as much as 150 meters off the bottom, most likely in response to movement of their prey (Atkinson 1989, Gauthier and Rose 2002). The three species are difficult to differentiate and, as a result, they are managed in the fishery as a single taxon. Analyses of parasites and genetic, meristic, and morphologic characteristics have been used to distinguish between *S. mentella* and *S. fasciatus* (Ni 1981, 1982, Kenchington 1986, Desrosiers et al. 1999, Marcogliese et al. 2003, Methot et al. 2004).

Many studies have tried to determine the reasons that fisheries collapse; however, there has been debate as to the principal cause (Hutchings and Myers 1994, Haedrich et al. 1995, Gomes et al. 1995, Myers et al. 1997, Bowering et al. 1997, Haedrich and Barnes 1997, Sinclair and Murawski 1997, Rose et al. 2000, Martínez 2003). Overfishing, predation, changes in prey availability and environmental factors have all been suggested as factors contributing to observed declines in size and abundance, and a long and ongoing debate concerns which of the many factors has played the greatest role. Examinations have ranged from descriptive (e.g., Villagarcia et al. 1999) to the broadly analytical (e.g., Bianchi et al. 2000) and from the application of local ecological knowledge (e.g., Neis et al. 1999) to quantitative ecosystem models based in theory (e.g., Martínez 2003). Most studies, however, have used traditional, standard statistical approaches (e.g., Myers et al. 1993). As would be expected, conclusions range across the

spectrum as to principal causes, but there is general agreement that the situation is complex with underlying dynamics operating at a number of scales.

Here I used two newer multivariate time series analytical techniques to determine whether complex dynamics in abundance can be described for a single species whose population units are distinctly defined. Trends in abundance were analyzed for six of the eight stock units of redfish *Sebastes spp.* in the Northwest Atlantic and the relationship between observed trends and external factors was explored. Distinct differences were expected as to which factors best explained the dynamics of each stock unit. The approaches I employed have been primarily used in the fields of economics and psychology (e.g., Molenaar 1985, 1989, 1993, Molenaar and de Gooijer 1988, Harvey 1989, Lütkepohl 1991, Molenaar et al. 1992, 1999) and only recently have been used to analyze zoobenthos and fisheries time series data (Solow 1994, Gaertner et al. 1999, Zuur et al. 2003a,b, CIESM 2004, Zuur and Pierce 2004, Erzini 2005, Erzini et al. 2005, Machias et al. 2006, Devine et al. 2007).

3.2. Methods

3.2.1. Data – response variables

Redfish data in the form of total number of individuals and number of mature individuals for *Sebastes fasciatus* and *S. mentella,* were taken from Department of Fisheries and Oceans (DFO) stock assessment research documents for five Northwest Atlantic population units: Unit 1, Unit 3, 2J3K, 3LN, and 3O (Figure 3.1, see Morin et al. (2004) for raw data); number of juveniles was then estimated as total minus mature individuals. In addition, EU surveys of the 3M (Flemish Cap) population were included

(see Ávila de Melo et al. (2005) for raw data). Data were available for both *S. mentella* and *S. fasciatus* for all population units except the Unit 3 stock, for which only data for *S. fasciatus* were available, and the 3M stock, where species were not differentiated. The Unit 1 stock includes redfish from NAFO Division 4RST and 3Pn4Vn January–March only (Atkinson and Power 1991). Data were for the years 1984–2002. Unit 1 was placed under moratorium in 1995 because of significantly low recruitment throughout the previous decade (Morin et al. 2004, Fréchet 2005). The Unit 1 population also contains heterozygous hybrids of the two species, but because their abundance was highly correlated with *S. mentella* abundance, they were omitted from the analysis here. Unit 2 redfish, another Laurentian Channel stock, also were not included in this analysis because only six years of data were available. Unit 3 redfish, the Scotian Shelf stock, were from NAFO Divisions 4WdehklX (Atkinson and Power 1991), 1970–2002, and the population is considered to be stable. The Grand Banks and Labrador populations consisted of three stock units defined geographically by NAFO Divisions, and referred to as the 3O (years 1973–2002), 3LN (1973–2002) and 2J3K (1978–2001) stocks (Parsons and Parsons 1973, Pinhorn and Parsons 1974, Power 2001, Morin et al. 2004). The 3O stock is still fished commercially, but the other two have been under moratorium since 1997 (2J3K) and 1998 (3LN). The 3O and 3LN stock estimates (inside Canadian waters) included spring and fall estimates of abundance; each was analyzed separately. Estimates of the 3O stock outside the Canadian 200-mile limit were available from Russian trawl surveys (Vaskov 2003). Morin et al. (2004), Méthot et al. (2004), and Power and Orr (2001) provide further details regarding determination of the stock units in Canadian waters and estimation of their abundance. The 3M stock (1989–2004) contains all three species, however, *S.*

mentella and *S. fasciatus* (the beaked redfishes) dominant the 3M catches and represent between 80%–90% of the total number of redfish caught (Saborido-Rey et al. 2004, Ávila de Melo et al. 2005).

For some population units, abundance estimates were not available for all years. Abundance for missing years was estimated as the average of one year before and one year after the missing data. Data were $\log_{10}$ transformed except 3O spring data, which was $\log_{10}(x+1)$ transformed because of zeros in the time series; all series were standardized by normalization to a mean of zero and a standard deviation of one.

3.2.2. Data – explanatory variables

Eleven external factors were used, including six environmental variables and five variables relating to exploitation. The North Atlantic Oscillation (NAO) Hurrell winter index (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) was used as a measure of the strength of large-scale atmospheric circulation. The NAO index changed from extreme negative to extreme positive values during the period from the mid-1960s to the mid-1990s (Visbeck et al. 2003). Positive anomalies are correlated with increased frequency and intensity of winter storms and northwesterly wind stress over the North Atlantic Ocean (Ottersen et al. 2001, Hurrell et al. 2003). Additionally, the NAO influences sea ice extent and melt, water temperature, the distribution and fluxes of major water masses and currents, deep water formation in the Greenland Sea, and intermediate water formation in the Labrador Sea (Colbourne et al. 1994, Dickson 1997, Curry et al. 1998, Hurrell et al. 2003). Mean sea surface temperature (SST) 0–100 meters was used excluding Cold Intermediate Layer waters, defined as waters between 30–150 meters and

less than 0° Celsius (Drinkwater 1996). Mean salinity (SAL) was estimated for depths 0–250 meters based on Dickson et al. (1988), who found that the effect of Great Salinity Anomalies (GSAs) on the Newfoundland-Labrador Shelf and eastern Grand Banks extended to approximately 300 meters depth. These salinity anomalies, which occur on a decadal scale, may be linked to changes in the NAO (Belkin et al. 1998, Hurrell et al. 2003). Three measures of mean bottom temperature were used, based on the primary depth range of the redfish species as specified in Morin et al. (2004): 100–700 meters (bottom temperature deep, BTD), 150–300 meters (bottom temperature shallow, BTS) and 350–500 meters (bottom temperature middle, BTM). Measures of exploitation obtained from the NAFO fisheries statistics database (www.nafo.ca) included days fished by the shrimp fishery (SHEFF), days fished by the redfish fishery (REDEFF), days fished by all fisheries where total redfish catch was at least 1% of the total catch 1960–2005 (FISHEFF), catch in the redfish fishery (REDCT), and total catch of redfish in all fisheries where catch was at least 1% of the total catch (CT). The shrimp fishery was emphasized because the by-catch of juvenile redfish is extremely high in this fishery (Alverson et al. 1994, Palmer and Sinclair 1997). All external factors were estimated for the area delineating each particular stock unit. Shrimp effort either did not exist or there were only a few years of data for NAFO Divisions 3LMNO and effort for those units was therefore omitted from the analyses. There were several years of missing effort and catch statistics in the NAFO database for population units, and the missing values were replaced with zeros. Zeros, and not means, were chosen for missing data based on the extremely low or zero catches or effort in the preceding and following years. Environmental data were also missing for some years for some population units; data for

these missing years were estimated as the mean between two adjacent years. Data were lagged up to eighteen years for populations 2J3K, Unit 1 and 3M, up to 13 years for population 3O and 3LN, and up to 10 years for the Unit 3 population. Some series could only be lagged 10–13 years because of the limited duration of the response series. The high numbers of lags were chosen based on generation time of redfish, estimated from age at 50% maturity and natural mortality to be 14.4 years for *S. fasciatus* (Laurel 2004) and approximately 14 years for *S. mentella* and *S. marinus* (Froese and Pauly 2006). All explanatory variables were standardized by normalization to a mean of zero and a standard deviation of one. Figures showing standardized explanatory variable time series for each population unit are in Appendix A and raw data are in Appendix B.

3.2.3. Time series methods

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) are multivariate methods designed specifically for shorter time series (at least 15–25 years) and are not burdened by many of the shortcomings of traditional time series analysis. They do not, for example, require long, stationary and complete time series and are relatively efficient at handling common trends.

MAFA, a type of principal component analysis for time series, can extract trends, estimate index functions and smooth data (Switzer and Green 1984, Shapiro and Switzer 1989, Solow 1994). Whereas PCA will produce axes (or components) across which the variance decreases, MAFA estimates axes that have decreasing autocorrelation with time lag 1. Because auto-correlation functions that decline slowly indicate a trend, the first MAFA axis is the main trend underlying the entire time series and other axes represent

less important trends. Trends are not linear. Randomization was used to obtain p-values in order to determine how many axes to use (Solow 1994). Loadings and canonical correlations, or cross-correlations between MAFA axes and response time series, were used to determine the relationship of response variables to MAFA axes. Cross-correlations were used to determine significant relationships between trends and explanatory variables.

DFA, a dimension reduction technique, can determine common patterns in time series, evaluate interactions between response variables, and determine the effects of explanatory variables (Zuur et al. 2003a,b). Furthermore, the effects of time lags in the explanatory variables can be evaluated explicitly. Akaike's information criterion (AIC) was used as an initial measure of goodness of fit and to compare models. Factor loadings were used to determine the importance of a trend to response variables. DFA has only recently been applied to fisheries data (Zuur et al. 2003b, Zuur and Pierce 2004, Erzini 2005, Erzini et al. 2005).

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) were fully described in Chapter 2.

3.3. Results

3.3.1. Unit 1

One main trend was identified by MAFA as significant for abundance of adults, juveniles, and combined juveniles/adults of both *Sebastes fasciatus* and *S. mentella* for the Gulf of St. Lawrence population, 1984–2002 (autocorrelation = 0.958, $p<0.001$, n = 6). The trend showed a decline from 1988 to 1996 that then stabilized (Figure 3.2). All

stages of both species were significantly correlated with the trend (significance level for correlations = 0.46, all correlations $\geq$ 0.75).

Both exploitation and environmental factors were correlated with the MAFA trend; lagged variables typically had higher correlations than unlagged variables. Only 2 out of 11 unlagged variables were significant (significance level for correlations = 0.46). External factors were lagged up to 18 years, resulting in 209 combinations of correlations with the MAFA trend. Ninety-one correlations were significantly different from zero at the 5% level, of which 10 could have been expected by chance alone. Correlation matrices are not presented here, but are available upon request. Environmental factors had fewer correlations than measures of exploitation and the correlations were weaker between environmental factors and the trend. Six environmental factors lagged up to 18 years had 15 significant correlations, while 5 exploitation factors lagged up to 18 years had 56 significant correlations with the MAFA trend. Bottom temperature (100–300 m) and sea surface temperature were correlated at high lags, and the remaining environmental factors were correlated at mid-range lags. Measures of exploitation were correlated at most lags for all measures.

A two-trend, two-explanatory factor model with redfish catch in the directed redfish fishery lagged 14 years and shrimp fishing effort lagged 9 years constituted the "best" DFA model (1 common trend AIC = 35.567, 2 common trend AIC = 35.560), based on a symmetrical, non-diagonal error covariance matrix. The difference in model fit based on the AIC value was extremely small; however, comparison of the elements of the error covariance matrix (**I**) for the one-trend versus two-trend model showed there was residual information remaining with the one-trend model (1 common trend, $\mathbf{I} \leq 0.35$; 2 common

trend, $\mathbf{I} \leq 0.16$). Therefore, a two-trend model was deemed "best". Common trends identified by DFA are not ranked in order of importance (Zuur and Pierce 2004), but their relative importance can be determined by comparison with MAFA trends. The first trend was an increase until 1991, followed by a decline until 1996 and then another increase; this trend was related to juveniles and combined juveniles/adults of both species (Figure 3.3). The second trend was an increase over the nineteen year time period. Factor loadings indicated adults of both species were negatively related to this trend (Figure 3.3). A negative correlation between the response series and a trend indicates the direction of the response variable is opposite of that depicted by the trend, i.e. abundance of adults actually declined over the time period. Estimated t-values for regressions indicated that all stages of *S. fasciatus* were strongly related to shrimp effort lagged 9 years, whereas juveniles of *S. mentella* were strongly related to redfish catch lagged 14 years (Table 3.1). Examination of plots of the two-trend, one-explanatory versus two-trend, two-explanatory fitted values (Figure 3.3) and model fits (AIC values) (Table 3.2) showed that including shrimp effort in the model improved the fit. The cross-correlation between redfish catch in the redfish fishery at lag 14 and shrimp fishing effort at lag 9 was not significant (correlation = 0.39, n = 2).

3.3.2. Unit 3

MAFA identified one main trend in relative abundance in Unit 3 (autocorrelation = 0.641, $p<0.001$, n = 3). The trend was a decline 1970–1979, followed by a general increase with some variation (Figure 3.2). Only *Sebastes fasciatus* is present in Unit 3;

adults, juveniles, and the combined juveniles/adults were significantly correlated with the trend (significance level for correlation = 0.35, all correlations $\geq$ 0.43).

External factors were lagged up to 10 years. Neither sea surface temperature, the NAO index, nor combined effort of all fisheries where redfish catch is at least 1% of the total harvest were correlated with this trend. Of the eight remaining external factors, environmental variables were highly correlated with the trend at mid-range lags whereas measures of exploitation were highly correlated at low and high lags. Most significant correlations were negative (28 out of 34 significant correlations). Measures of exploitation produced a greater number of significant correlations than environmental factors. Out of 121 correlations, 34 were significantly different from zero at the 5% level, of which 6 could have been expected by chance alone.

The "best" model in terms of lowest AIC value was a one-trend, two-explanatory variable model with bottom temperature (350–500 m) lagged 1 year and catch of redfish in all fisheries lagged 3 years (AIC = 134.2). The trend was a decrease until 1980, followed by an increase to 1997 after which it again declined (Figure 3.4). Only juveniles of *S. fasciatus* were strongly related to this trend (Figure 3.4). Examination of the error covariance matrix indicated a large amount of residual information remaining for adults and combined juveniles/adults ($\mathbf{I} \leq 0.77$); however, there was no other trend in the data (i.e. the second trend was a flat line). Estimated regression parameters showed only juveniles were strongly related to bottom temperature; no indices were strongly related with catch lagged 3 years (Table 3.3). The general absence of strong relationships could indicate that the model was inappropriate; however, model fits versus observed values showed that the fit of the model was improved slightly for all three stages by adding

redfish catch (all fisheries) (Figure 3.4). Examination of model fits (AIC values) (Table 3.4) showed that the one-trend, two-explanatory model was 'better' than a one- or no-explanatory variable model. The cross-correlation between bottom temperature (350–500 m) at lag 1 and catch at lag 3 was significant (correlation = 0.47).

Because the first model indicated unexplained information remained, the second "best" model was assessed. This was a one-trend, two-explanatory model using bottom temperature (350–500 m) lagged 5 years and redfish catch in all fisheries lagged 3 years (AIC = 134.6); no other trend was present in the data. Again, elements of the error covariance matrix were quite large, indicating residual information ($\mathbf{I} \leq 0.68$). The trend was the same as described for the first DFA model; however, factor loadings indicated that all indices (juvenile, adult and combined juveniles/adults) for *S. fasciatus* were related to the trend (Figure 3.5). Estimated regression parameters showed that adults and combined juveniles/adults were strongly related to bottom temperature lagged 5 years; again, no index was strongly related with catch lagged 3 years (Table 3.5). Plots of model fits versus observed values indicated that the addition of catch to the model did not improve the fit for juveniles, but did improve the fit for adults and combined juveniles/adults for the beginning of the time series (Figure 3.5). Examination of model fits (Table 3.6) showed that a one-trend, two-explanatory model was again 'better' than a one- or no- explanatory variable model. Another 15 one-trend, two-explanatory models were examined, but model fit was consistently poorer and less residual information was explained with each new "best" model. The cross-correlation between bottom temperature (350–500 m) at lag 5 years and catch at lag 3 years was not significant (correlation = 0.18, n = 2).

3.3.3. Population 3O

Three abundance indices were available for the 3O redfish populations and included estimates based on the Canadian spring survey, Canadian autumn survey, and Russian survey outside Canada's 200-mile EEZ. MAFA indicated there were no significant trends in the data from the autumn or Russian surveys (autocorrelation autumn survey = 0.65, p=0.669, n = 6; autocorrelation Russian survey = 0.11, p=0.232, n = 2). Low autocorrelations, such as that seen using the Russian survey, indicate that the trend is a collection of the noise components in the series (see Chapter 2); therefore, the Russian data is not discussed further. The autocorrelation was relatively high for abundance based on Canadian autumn surveys, but the trend was not significantly related to either *Sebastes fasciatus* (correlations range -0.15–0.22, significance level for correlations = 0.58) or *S. mentella* (correlations range 0.43–0.51, significance level for correlations = 0.58) and also will not be discussed further.

MAFA indicated two significant trends in abundance estimates from the Canadian spring surveys (Figure 3.2). The main trend (autocorrelation = 0.91, $p<0.001$, n = 6) was an increase over time, which was most pronounced beginning in 1990 and then declined in 2000–2002. The main trend was significantly correlated with both species, juveniles, adults and the combined population (significance level for correlations = 0.37, all correlations $\geq$ 0.44). The second trend showed decadal oscillations (autocorrelation = 0.64, p=0.007, n = 6) and was significantly correlated with all combinations except adults of *Sebastes fasciatus* and *S. mentella* (significance level for correlations = 0.37).

External factors were lagged up to 13 years. Shrimp fishing effort was not available for 3O. Sea surface temperature and bottom temperature (100–700 m) were not correlated with the first trend and the other two measures of bottom temperature were only significantly correlated with this trend at lag 1 year (correlation = 0.46, both variables). Salinity and the NAO index were significantly correlated to the first trend at low and mid-range lags, whereas measures of exploitation were significantly correlated at most lags. Effort for the redfish fishery (positively correlated) and combined effort of all fisheries where redfish catch is $\geq$ 1% of the total catch (negatively correlated) were significantly correlated to the first trend at all lags (all correlations ranged -0.42– -0.61, significance level for correlations = 0.37). Shallow and middle bottom temperatures were not significantly correlated with the second trend and bottom temperature (100–700 m) was significantly correlated in only one case (lag 13, correlation = 0.42). Only six significant correlations were found between environmental variables and the second trend, whereas measures of exploitation had 17 significant correlations with MAF2 at low and mid-range lags. Fishing effort for all fisheries where redfish catch was $\geq$ 1% of the total catch had the highest number of significant correlations (10), all of which were negative. Eighty-four of 280 correlations were significantly different from zero at the 5% level, of which 14 could be expected by chance alone.

The best model indicated by DFA was a two-trend, two-explanatory variable model, with salinity lagged 4 years and redfish catch in all fisheries where redfish is $\geq$ 1% of the total catch lagged 12 years, based on a symmetrical, non-diagonal error covariance matrix (1 common trend AIC = 141.3, 2 common trends AIC = 130.0). Examination of model fits (Table 3.7) showed that a one-trend, two-explanatory model was 'better' than a one-

or no- explanatory variable model. In addition to having a poorer fit, examination of the elements from the error covariance matrix for the one-trend model indicated that there was substantial residual information not explained by the model ($\mathbf{I} \leq 0.6$). The elements from the two-trend model were small ($\mathbf{I} \leq 0.1$) except for *Sebastes fasciatus* adults ($\mathbf{I} = 0.49$), indicating that the two-trend was the better model.

The two trends identified by DFA were nearly identical to the trends identified by MAFA. The main trend was an increase until 1999 and then a steep decline (Figure 3.6). Factor loadings indicated that all species and lifestages except *S. fasciatus* juveniles and combined juveniles/adults were strongly related to this trend (Figure 3.6). The second trend was a steady increase that oscillated strongly on a decadal scale, with peaks in 1984 and 1994 (Figure 3.6). Factor loadings indicated *S. fasciatus* juveniles and combined juveniles/adults were very strongly related to this trend. Regression parameters showed that adding salinity lagged 4 years improved the model fit for juveniles and combined juveniles/adults of *S. fasciatus* (Table 3.8). Adding redfish catch in all fisheries lagged 12 years improved the model fit for all lifestages of *S. mentella* (Table 3.8, Figure 3.6). Neither explanatory factor improved the model fit for adults of *S. fasciatus* (Table 3.8). Inspection of model fits to observed values showed that including redfish catch in all fisheries to the two-trend, one-explanatory variable model improved the fit of the model for all indices except *S. fasciatus* adults (Figure 3.6). The cross-correlation between salinity at lag 4 and catch at lag 12 was not significant (correlation = -0.09, n = 2).

3.3.4. Population 3LN

Abundance estimates from the Canadian spring and autumn surveys were available for the 3LN redfish population. MAFA indicated two significant trends for abundance estimates from the spring survey (MAF 1 autocorrelation = 0.94, $p<0.001$, n = 6; MAF 1 autocorrelation = 0.80, $p<0.001$, n = 6) and one significant trend for estimates from the autumn survey (autocorrelation = 0.94, p = 0.04, n = 6; Figure 3.2).

The main trend from the spring survey data was relative stability until 1990, an abrupt increase until 1993 and a return to stability to 2002 (Figure 3.2). *S. mentella*, adults, juveniles and combined juveniles/adults, were significantly correlated with this trend (correlations ≥ 0.75, significance level for correlations = 0.37). No shrimp effort was available for 3LN. All external factors were highly correlated with MAF1 for spring survey abundance estimates at mainly low and high lags; mid-range lags were not significant for any factor (significance level for correlations = 0.37, all correlations were < 0.37). Environmental and exploitation factors had a similar proportion of significant correlations; environmental factors had 37 significant correlations and exploitation had 25. Out of 138 correlations, 62 were significantly different from zero at the 5% level, of which 7 could be expected by chance alone.

The second trend in data from the spring survey identified three oscillations, with minima in 1985 and 1994 (Figure 3.2). Only adults of *S. fasciatus* were significantly correlated with this trend (correlation = 0.66); *S. fasciatus* juveniles were not correlated with either trend. All external factors except middle bottom temperature were significantly correlated, at mid-range lags only, with the second trend in spring survey

estimated abundance. Measures of exploitation had a higher proportion of significant correlations (63%) than environmental variables (37%). Of 138 correlations, 48 were significantly different from zero at the 5% level, of which 7 could be expected by chance alone.

From fall survey estimates of relative abundance, the only trend identified by MAFA was an increase that stabilized in 1994 (Figure 3.2). Only *S. mentella* adults were significantly correlated with this trend (correlation = 0.69, significance level for correlations = 0.60). All external factors were highly correlated at various lags with MAF1 from autumn survey abundance estimates. Environmental factors were often significantly correlated at low lags, whereas exploitation was significantly correlated at high and low lags (significance level for correlations = 0.60). More measures of exploitation were significantly related to this trend than were environmental factors; 39 measures of exploitation and only 17 measures of environmental were significant. Of 139 correlations, 56 were significantly different from zero at the 5% level, of which 7 could be expected by chance alone.

Symmetrical, non-diagonal error covariance matrix models represented the best model option for 3LN spring survey abundance estimates. The "best" DFA model was a two-trend, two-explanatory model using the NAO winter index lagged 2 years and sea surface temperature lagged 6 years (1 common trend AIC = 65.3, 2 common trends AIC = 51.0). The error covariance matrix for the two trend model indicated there was residual information remaining ($\mathbf{I} \leq 0.48$), but when a third trend was added, it was a straight line (i.e. no additional trends were in the data). Examination of model fits (AIC value) showed a two-trend, two-explanatory model had the best fit (Table 3.9). The first trend was

similar to the main trend identified by MAFA; the values increased slightly until 1981, decreased until 1987, and then increased abruptly (Figure 3.7). Factor loadings indicated only *S. mentella* (all indices) was related to this trend (Figure 3.7). The second trend showed an increase with substantial variation until 1994, an abrupt decrease until 1999, and then a slight increase (Figure 3.7). Factor loadings indicated juveniles of both species were positively related to this trend and *S. fasciatus* adults were negatively correlated (Figure 3.7). Negative relationships between a response time series and the trend indicates the trend for that species is the opposite of that depicted in the figure, i.e. *S. fasciatus* adults declined until 1994 and then abruptly increased. Estimated t-values for regressions indicated that all indices for *S. fasciatus* were strongly related to the NAO index lagged 2 years (t-values $\geq$ -3.14) and all indices for both species were strongly related to sea surface temperature lagged 6 years (Table 3.10). The two-trend model was improved slightly for adults towards the end of the time series by adding sea surface temperature, while the model fit improved for all other indices near the middle of the time series (Figure 3.7). The cross-correlation between NAO at lag 2 and sea surface temperature at lag 6 was not significant (correlation = -0.01, n = 2).

Only one trend was found in autumn survey abundance estimates (AIC = 13.4). Elements of the non-diagonal error covariance matrix indicated slightly high values for two response series (**I** = 0.29, 0.36); adding another trend did not reduce the amount of residual information available, but it did increase the AIC value (AIC = 23.1, Table 3.11). Therefore, a one-trend, two-explanatory variable model was used, with bottom temperature (100–700 m) lagged 7 years and sea surface temperature lagged 3 years. The trend was an increase in abundance until 1995, followed by a plateau (Figure 3.8).

Canonical correlations indicated the trend was related to abundance of adults of both species and combined juveniles/adults of *S. mentella* (Figure 3.8). Estimated regression parameters showed that all indices for both species were strongly related with bottom temperature (100–700 m) lagged 7 years, and abundance of *S. fasciatus* adults and combined juveniles/adults were strongly related with sea surface temperature lagged 3 years (Table 3.12). Inspection of the model fit plots showed that adding sea surface temperature improved the model fit for *S. fasciatus* and *S. mentella* juveniles for the first two years of the series (Figure 3.8). The cross-correlation between bottom temperature lagged 7 years and sea surface temperature lagged 3 years was not significant (correlation = -0.03, n = 2).

3.3.5. Population 2J3K

Two trends in abundance for the 2J3K population were identified by MAFA (Figure 3.2). The main trend was a decline until 1992, after which abundances stabilized (autocorrelation = 0.91, $p<0.001$, n = 6). Abundance of juveniles, adults and combined juveniles/adults of both *Sebastes fasciatus* and *S. mentella* were significantly correlated to this trend (correlations $\geq$ 0.59, significance level for correlations = 0.41). The second trend was a steeper decline until 1985, abundance stabilized until 1995 after which it increased abruptly (autocorrelation = 0.93, $p<0.001$, n = 6). Only abundance of juveniles of *S. fasciatus* and *S. mentella* were significantly correlated with MAF2 (correlations $\geq$ 0.62).

Nine of the eleven external factors were highly correlated with MAF1; shallow and deep bottom temperatures were not correlated with this trend (correlations $\leq$ 0.41).

Bottom temperature (350–500 m) and the NAO winter index had 19 significant correlations with the first trend, and the remaining environmental factors had 10. Nearly all lags for measures of exploitation were significantly correlated with MAF1; exploitation had 78 significant correlations in all. The proportion of significant correlations to the second trend was again greater for measures of exploitation (76%) than for environmental factors (24%); fishing effort for the redfish fishery had the highest number of significant correlations (9). Of 418 correlations, 152 were significantly different from zero at the 5% level, 20 of which could be explained by chance alone.

The best DFA model was a two-trend, two-explanatory variable model, with sea surface temperature lagged 6 years and redfish catch in the redfish fishery lagged 4 years, based on a symmetrical, non-diagonal error covariance matrix (1 common trend AIC = 57.3, 2 common trends AIC = 48.2). In addition to a higher AIC value, examination of the elements from the error covariance matrix for the one-trend model indicated that there was residual information not explained by the model ($\mathbf{I} \leq 0.5$). The elements from the two-trend model were small ($\mathbf{I} < 0.01$) and the model fit improved with the addition of a second trend (Table 3.13), indicating a better model. The two trends identified by DFA were identical to the trends identified by MAFA. The main trend was a decline until 1994 followed by an increase, whereas the second trend was a more precipitous decline in the early years of the series followed by an increase beginning in the early 1990s (Figure 3.9). Factor loadings indicated that adults and combined juveniles/adults were strongly related to the first trend, whereas juveniles and combined juveniles/adults were highly correlated with the second trend (Figure 3.9). Examination of regression parameters showed that adults and combined juveniles/adults of both species were strongly related to

sea surface temperature lagged 6 years and all abundances except *S. fasciatus* juveniles were strongly related to redfish catch in the redfish fishery lagged 4 years (Table 3.14). Adding redfish catch to the two-trend model improved the fit of the model for all indices, especially towards the middle and end of the time series, except for *S. fasciatus* juveniles (Figure 3.9). Cross-correlation between sea surface temperature at lag 6 and catch at lag 4 was significant (correlation = 0.45, n = 2).

3.3.6. Population 3M

The one significant trend identified by MAFA for abundance of the 3M redfish population unit was an increase to 1994, a decline to 1999, and then an increase (autocorrelation = 0.75, p=0.009, n = 3, Figure 3.2). Redfish were not identified to species for this population (see Methods). Juveniles, adults, and combined juveniles/adults were significantly correlated with this trend (all correlations $\geq |0.54|$, significance level for correlations = 0.50). Adults were negatively correlated with the trend (correlation = -0.54), indicating abundance actually decreased until 1994, increased until 2000, and then decreased thereafter.

Fishing effort for shrimp was not available for this population. Bottom temperature (100–700 m) and salinity were not significantly correlated (all correlations ≤ 0.50) with the trend. The proportion of significant correlations was greater for measures of exploitation (61%) than for environmental factors (39%). Exploitation was significantly correlated at mid-range and high lags, whereas environmental factors were generally significantly correlated only at only high lags. Of 190 correlations, 23 were significant at the 5% level, of which 10 could be expected by chance alone.

The "best" DFA model was a one-trend, two-explanatory variable model with bottom temperature (350–500 m) lagged 1 year and catch of redfish in all fisheries lagged 10 years (AIC = 1.84). A non-diagonal, symmetrical covariance error structure was used. Analysis of the elements of the error covariance matrix indicated there was little residual information left unexplained by the one-trend DFA model ($\mathbf{I} \leq 0.2$). The model was vastly improved by adding a second explanatory factor (Table 3.15). The trend was the same as that found by MAFA; abundance increased to 1994, declined to 1999, and then increased (Figure 3.10). Factor loadings indicate that juveniles and combined juveniles/adults were positively and adults negatively related to this trend (Figure 3.10). Estimated t-values for regressions indicated that combined juveniles/adults were strongly related with bottom temperature (350–500 m) and catch (all fisheries) lagged 10 years (Table 3.16). Adding catch to the two-trend model improved the fit of the model for the three indices after 1995 (Figure 3.10). The cross-correlation between bottom temperature lagged 1 year and catch lagged 10 years was not significant (correlation = -0.13, n = 2).

3.4. Discussion

Population units of redfish *Sebastes spp.* in the Northwest Atlantic exhibit very different trends in abundance; some populations have supported sustainable fisheries, while others have had moratoria imposed (Morin et al. 2004, Fréchet 2005). Different environmental factors, at least on the Scotian Shelf and in the Gulf of St. Lawrence, were thought to partially explain the differences seen between populations (Gascon 2003). Two methods of multivariate analyses have shown that the trends for most populations are related to a combination of environmental and exploitation factors. MAFA has shown that

measures of exploitation, including lags, were most frequently correlated significantly with trend in redfish abundance for all populations except 3LN. DFA condensed the available information to factors that explained the most residual information (see Methods for explanation), and indicated which combination of factors was related to the trends (Figure 3.11). Trends in the 3LN population were mostly related to environmental factors (Figure 3.11), which is not surprising given that this population inhabits a region influenced by the Labrador Current flowing from the north and anomalies resulting from Gulf Stream influences on the Tail of the Grand Bank (Drinkwater 1996). Trends in abundance of redfish in Unit 1 were mostly related to exploitation (Figure 3.11). Fishing effort in the Gulf of St. Lawrence was high in the early and late 1990s compared to the mid-1990s (Kulka and Pitcher 2001), and by-catch and discards of juvenile redfish in the shrimp fishery have been high since the 1970s (Palmer and Sinclair 1997). A mixture of environmental factors and exploitation is related to trends in all remaining populations (Figure 3.11).

Recent studies have proposed that observed changes in fish populations are the result of multiple factors that act in combination but at different scales (Zwanenburg 2000, Devine et al. 2007, Shelton et al. 2006). I found that exploitation and environmental factors on different temporal scales are related to the trends in redfish populations in the Northwest Atlantic as well (Figure 3.12). Exploitation affected all populations at multiple temporal scales (Figure 3.12), which was not surprising given the indiscriminate nature of most of the fisheries focused on in this study. Most groundfish fisheries utilize large benthic otter trawls, a gear type not known for its selectivity. In addition to direct removals of individuals, bottom trawling is responsible for alteration and destruction of

bottom habitat (Watling and Norse 1998, Turner et al. 1999, Kaiser et al. 2000), including damage to the cold-water coral forests with which redfish are often associated (Husebø et al. 2002, Fosså et al. 2002, Auster et al. 2003, Roberts et al. 2006). The shrimp fishery, because it uses a small mesh size, has the highest by-catch rate of any fishery (Alverson et al. 1994). Populations on the Flemish Cap and northern Newfoundland-Labrador Shelf are affected by environmental factors that operate on longer temporal scales than in more southern populations (Scotian Shelf, Gulf of St. Lawrence, and 3O, Figure 3.12), possibly as a result of the differing water masses that characterize these areas (Helbig et al. 1992). The Newfoundland-Labrador Shelf and Flemish Cap are greatly influenced by the cold, polar waters of the Labrador Current (Lazier 1982, Drinkwater and Harding 2001), whereas the other regions are influenced by the warm waters of the Gulf Stream, slope waters, and the St. Lawrence River outflow (DFO 1998, Zwanenburg 2003). The 3LN population could be considered intermediate in its response because it is affected by both the Labrador Current and Gulf Stream, and a wide range of temporal scales might therefore influence these stocks (Figure 3.12). The analyses show that environmental factors are related at all temporal scales for this population, although closer examination also reveals interspecific differences. *S. fasciatus* is highly related to environmental factors operating at mid-range scales, while *S. mentella* is related to factors operating at short and long temporal scales. Although the spring survey does not sample the entire range of the 3LN population for *S. mentella* (Morin et al. 2004), results from the autumn survey, which extends deeper, again show that environmental factors are related to the *S. mentella* abundance trend at both long and short time scales. Related species in the same

genus can respond differently to external factors, as found by Moser and Boehlert (1991) for several *Sebastes spp.* in the Pacific Ocean.

Off the Grand Bank, populations of *S. mentella* and *S. fasciatus* appear to operate out-of-phase with each other. As *S. fasciatus* populations declined in the late 1970s and again in the 1980s, *S. mentella* increased. This pattern is similar to sardine and anchovy populations in the Pacific Ocean, which alternate cycles in response to environmentally-driven food availability and large-scale atmospheric factors (Bakun and Broad 2003, Chavez et al. 2003, Lecomte et al. 2004). Time series of fish abundance are known to combine high-frequency oscillations as a result of interactions between individuals and species and the indirect effects of environmental variability. Other contributing factors are low-frequency oscillations and trends, which are related to exploitation, climatic and oceanic changes, and large-scale atmospheric changes (Bjørnstad and Grenfell 2001).

A broad range of factors operate on various temporal scales to influence trends in *Sebastes spp.* abundance in the Northwest Atlantic. Currently, management tends to focus on stock trends over a very short time scale of the last few years. There is very little consideration of long-term trends or the delayed effects of external factors. Reactions to external factors will not appear for years or even decades if the rate of change is slow, effects are temporarily stored before spreading through the system (Jørgensen 2002, Fath 2004), or if the fishery is based on only a few year classes. For species such as redfish that grow slowly, mature late, and have low fecundity (Koslow et al. 2000), changes may not appear for one to several generations and when they occur it may be very difficult to pinpoint the causal factor. Management strategies for redfish in the Northwest Atlantic must take into consideration the individual population responses to environmental factors

and exploitation, including consideration of the temporal scales at which these factors operate.

For the Unit 1 redfish population, exploitation is a key factor. The redfish fishery was closed in 1995 and these analyses indicate no change in the trend for adults of that population, most likely because the effect of exploitation on this population operates on a long temporal scale. Unit 1 redfish may have been overfished to the point where recovery will not occur for several generations, especially given that juveniles are still taken in large numbers as by-catch in the shrimp fishery. Exploitation and by-catch may do much more than affect abundance directly through removals of individuals. Leaman (1991) found that Pacific *Sebastes alutus* from heavily exploited stocks were less fecund than fish of the same size in lightly exploited stocks.

The Scotian Shelf (Unit 3) redfish population may be successful because it has not been overexploited. In addition, bottom temperature is important in explaining the success of this population. Bottom waters on the Scotian Shelf are among the most variable in the North Atlantic (Zwanenburg 2003). Currently, bottom temperatures show an increasing trend, which could benefit this population. Other factors not included in this study may also be responsible for trends found in the Scotian Shelf and southern Grand Bank (3O) populations; DFA indicated there was a lot of residual information left unexplained in models for these units.

The 3O stock currently supports a small fishery. Analyses indicate that both redfish catch in all fisheries and salinity were important for this population. Reducing the amount of redfish taken in other fisheries may be key for continued success of this population. Other factors, such as the observed interaction between species, may also be important for

this population and should be explored further. Indirect and hard to measure factors, such as competition, may better explain the dynamics of this population than environment or exploitation.

The cyclic out-of-phase pattern in abundance displayed by both species should also be taken into consideration for the management of the 3LN stock. Environment has been shown to be important for this stock, particularly the NAO. The NAO has been shown to influence the latitudinal position of the Gulf Stream (Taylor and Stephens 1998). *S. mentella* abundance, based on estimates that cover its depth range, has shown an increasing trend that occurred after effort lessened in 1994 outside the Canadian EEZ (Ávila de Melo et al. 2005). This pattern could indicate that this population may be able to recover much more quickly from over-exploitation than other populations or that it had not been exploited past "the point of no return". Assessments indicate that the stock is showing some recovery; mean length of fish and spawner biomass, though variable, are increasing (Ávila de Melo et al. 2005).

Adults in the 2J3K population are beginning to show a slight increase. A moratorium has been in place since 1997 and fishing effort has been relatively low since 1992, except for by-catch in the shrimp fishery. Although recruitment has been poor for 25 years and annual consumption by seals is estimated to be 175 million juvenile redfish (Morin et al. 2004), juveniles also increased in abundance beginning in the mid-1990s. Roques et al. (2002) postulated that the Irminger Sea redfish population may "seed" the 2J3K stock with larvae.

I have shown that complex dynamics occur at the stock level over relatively small spatial and temporal scales. Moratoria for three of the redfish populations have been in

place for approximately 10 years and only recently have these populations begun to show any sign of improvement. These patterns support the argument that deep-sea populations cannot be managed at the same scale as shelf fisheries.

Here I have explored two methods of time series analyses and determined that they can be quite useful and informative. In the next chapter, I begin to explore trends in other species, focusing on deep-sea fishes. Before using these techniques on deep-sea species, I wanted to determine if the data were adequate to describe trends in "non-traditional" fishery species; I achieve this objective using generalized linear modeling.

Table 3.1. Estimated regression parameters, standard errors and t-values for the two-trend, two-explanatory factor DFA model for abundance of the Unit 1 (Gulf of St. Lawrence) *Sebastes spp.* population unit, 1984–2002. **D** was explained in Chapter 2.

	Shrimp fishing effort lagged 9 years			Redfish catch in the redfish fishery lagged 14 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
S. fasciatus						
All	0.42	0.18	2.30	0.00	0.09	-0.03
Juveniles	0.54	0.22	2.46	-0.03	0.13	-0.23
Adults	0.32	0.13	2.52	0.06	0.07	0.91
S. mentella						
All	0.10	0.16	0.64	0.01	0.08	0.19
Juveniles	0.36	0.21	1.69	-0.38	0.11	-3.38
Adults	-0.17	0.14	-1.18	0.10	0.06	1.61

Table 3.2. Values of Akaike's information criterion (AIC) for DFA models with 2 trends and different sets of explanatory variables (exp), based on a symmetrical, non-diagonal covariance matrix for abundance of the Unit 1 (Gulf of St. Lawrence) *Sebastes spp.* population unit, 1984–2002. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		64.3
2 trend		74.1
Relative abundance + exp + noise		
1 trend	Redfish catch lagged 14 years	56.1
1 trend	Shrimp effort lagged 9 years	45.6
1 trend	Redfish catch 14 & shrimp effort 9	35.567
2 trend	Redfish catch 14 & shrimp effort 9	**35.560**

Table 3.3. Estimated regression parameters, standard errors and t-values for the first "best" one-trend, two-explanatory factors DFA model for abundance of the Unit 3 (Scotian Shelf) stock of *Sebastes fasciatus*, 1970–2002. **D** was explained in Chapter 2.

	Bottom temperature (350–500m) lagged 1 year			Redfish catch (all fisheries) lagged 3 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
Adults	-0.28	0.18	-1.6	0.32	0.19	1.71
Juveniles	0.42	0.10	4.37	-0.29	0.22	-1.33
All	-0.18	0.16	-1.11	0.31	0.19	1.61

Table 3.4. Values of Akaike's information criterion (AIC) for DFA models with 1 trend and different sets of explanatory variables (exp), based on a symmetrical, non-diagonal covariance matrix for abundance of the Unit 3 (Scotian Shelf) stock of *Sebastes fasciatus*, 1970–2002. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		148.5
2 trend		No second trend
Relative abundance + exp + noise		
1 trend	Bottom temperature (350–500m) lagged 1 year	152.2
1 trend	Redfish catch (all fisheries) lagged 3 years	141.2
1 trend	Bottom temperature (350–500m) 1 & Redfish catch (all fisheries) 3	**134.2**

Table 3.5. Estimated regression parameters, standard errors and t-values for the second "best" one-trend, two-explanatory factors DFA model for abundance of the Unit 3 (Scotian Shelf) stock of *Sebastes fasciatus*, 1970–2002. **D** was explained in Chapter 2.

	Bottom temperature (350–500m) lagged 5 years			Redfish catch (all fisheries) lagged 3 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
Adults	0.36	0.15	2.31	0.25	0.19	1.33
Juveniles	-0.12	0.11	-1.04	-0.05	0.19	-0.27
All	0.36	0.14	2.55	0.30	0.20	1.48

Table 3.6. Values of Akaike's information criterion (AIC) for DFA models with 1 trend and different sets of explanatory variables (exp), based on a symmetrical, non-diagonal covariance matrix for abundance of the Unit 3 (Scotian Shelf) stock of *Sebastes fasciatus*, 1970–2002. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		148.5
2 trend		No second trend
Relative abundance + exp + noise		
1 trend	Bottom temperature (350–500m) lagged 5 years	146.4
1 trend	Redfish catch (all fisheries) lagged 3 years	141.2
1 trend	Bottom temperature (350–500m) 5 & Redfish catch (all fisheries) 3	**134.6**

Table 3.7. Values of Akaike's information criterion (AIC) for DFA models with 2 trends and different sets of explanatory variables (exp), based on a symmetrical non-diagonal covariance matrix for abundance from the spring survey of the 3O *Sebastes spp.* population unit, 1973–2002. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		154.4
2 trend		150.5
Relative abundance + exp + noise		
1 trend	Salinity lagged 4 years	142.2
1 trend	Redfish catch (all fisheries) lagged 12 years	154.6
1 trend	Salinity lagged 4 yrs & Redfish catch (all fisheries) lagged 12 yrs	141.3
2 trend	Salinity lagged 4 yrs & Redfish catch (all fisheries) lagged 12 yrs	**130.0**

Table 3.8. Estimated regression parameters, standard errors and t-values for the two-trend, two-explanatory factor DFA model for abundance from the spring survey of the 3O *Sebastes spp.* population unit, 1973–2002. **D** was explained in Chapter 2.

	Salinity lagged 4 years			Redfish catch in all fisheries lagged 12 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
S. fasciatus						
All	-0.31	0.10	-2.94	0.17	0.11	1.52
Juveniles	-0.28	0.09	-3.07	0.22	0.10	2.31
Adults	-0.23	0.14	-1.69	0.02	0.14	0.12
S. mentella						
All	0.08	0.06	1.38	0.29	0.06	4.66
Juveniles	0.18	0.08	2.28	0.25	0.08	3.05
Adults	-0.06	0.06	-0.93	0.21	0.07	3.20

Table 3.9. Values of Akaike's information criterion (AIC) for DFA models with 2 trends and different sets of explanatory variables (exp), based on a symmetrical non-diagonal covariance matrix for abundance from the spring survey of the 3LN *Sebastes spp.* population unit, 1973–2002. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		94.7
2 trend		79.2
Relative abundance + exp + noise		
1 trend	NAO lagged 2 years	76.2
1 trend	Sea surface temperature lagged 6 years	75.4
1 trend	NAO lagged 2 years & Sea surface temperature lagged 6 years	65.3
2 trend	NAO lagged 2 years & Sea surface temperature lagged 6 years	**51.0**

Table 3.10. Estimated regression parameters, standard errors and t-values for the two-trend, two-explanatory factor DFA model for abundance from the spring survey of the 3LN *Sebastes spp.* population unit, 1973–2002. **D** was explained in Chapter 2.

	NAO lagged 2 years			Sea surface temperature lagged 6 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
S. fasciatus						
All	-0.47	0.13	-3.55	-0.47	0.13	-3.52
Juveniles	-0.43	0.14	-3.14	-0.42	0.14	-3.06
Adults	-0.43	0.11	-3.86	-0.43	0.11	-3.82
S. mentella						
All	-0.10	0.09	-1.00	-0.29	0.09	-3.13
Juveniles	-0.07	0.11	-0.62	-0.33	0.11	-3.01
Adults	-0.09	0.08	-1.10	-0.22	0.08	-2.72

Table 3.11. Estimated regression parameters, standard errors and t-values for the two-trend, two-explanatory factor DFA model for abundance from the autumn survey of the 3LN *Sebastes spp.* population unit, 1991–2001. **D** was explained in Chapter 2.

	Bottom temperature 100–700m lagged 7 years			Sea surface temperature lagged 3 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
S. fasciatus						
All	-0.50	0.16	-3.06	0.51	0.16	3.09
Juveniles	-0.50	0.19	-2.66	0.45	0.19	2.44
Adults	-0.40	0.13	-3.16	0.45	0.13	3.43
S. mentella						
All	-0.77	0.13	-5.72	0.03	0.14	0.19
Juveniles	-0.55	0.21	-2.62	0.33	0.21	1.58
Adults	-0.67	0.15	-4.39	-0.19	0.15	-1.23

Table 3.12. Values of Akaike's information criterion (AIC) for DFA models with 2 trends and different sets of explanatory variables (exp), based on a symmetrical non-diagonal covariance matrix for abundance from the autumn survey of the 3LN *Sebastes spp.* population unit, 1991–2001. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		95.0
2 trend		100.6
Relative abundance + exp + noise		
1 trend	Bottom temperature 100–700m lagged 7 years	68.9
1 trend	Sea surface temperature lagged 3 years	75.9
1 trend	Bottom temperature 100–700m 7 & Sea surface temperature 3	**13.4**
2 trend	Bottom temperature 100–700m 7 & Sea surface temperature 3	23.1

Table 3.13. Values of Akaike's information criterion (AIC) for DFA models with 2 trends and different sets of explanatory variables (exp), based on a symmetrical non-diagonal covariance matrix for abundance of the 2J3K *Sebastes spp.* population unit, 1978–2001. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		107.2
2 trend		90.2
Relative abundance + exp + noise		
1 trend	Sea surface temperature lagged 6 years	74.8
1 trend	Redfish catch (redfish fishery) lagged 4 years	63.6
1 trend	Sea surface temperature 6 & Redfish catch (redfish fishery) 4	57.3
2 trend	Sea surface temperature 6 & Redfish catch (redfish fishery) 4	**48.2**

Table 3.14. Estimated regression parameters, standard errors and t-values for the two-trend, two-explanatory factor DFA model for abundance of the 2J3K *Sebastes spp.* population unit, 1978–2001. **D** was explained in Chapter 2.

	Sea surface temperature lagged 6 years			Redfish catch (redfish fishery) lagged 4 years		
	Estimated value from **D**	Standard error	t-value	Estimated value from **D**	Standard error	t-value
S. fasciatus						
All	-0.20	0.08	-2.63	0.32	0.12	2.72
Juveniles	-0.06	0.09	-0.67	-0.01	0.14	-0.06
Adults	-0.16	0.07	-2.36	0.33	0.10	3.29
S. mentella						
All	-0.21	0.06	-3.33	0.46	0.11	4.35
Juveniles	-0.04	0.10	-0.36	0.55	0.16	3.42
Adults	-0.21	0.05	-3.97	0.45	0.09	4.78

Table 3.15. Values of Akaike's information criterion (AIC) for DFA models with 1 trend and different sets of explanatory variables (exp), based on a symmetrical non-diagonal covariance matrix for abundance of the 3M *Sebastes spp.* population unit, 1989–2004. Bold type indicates the best model chosen for the analysis. The number appended to the explanatory variable indicates the lag in years.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend		98.8
2 trend		No trend
Relative abundance + exp + noise		
1 trend	Bottom temperature 350–500m lagged 1 year	84.9
1 trend	Catch (all fisheries) lagged 10 yrs	93.4
1 trend	Bottom temperature 350–500m 1 & Catch (all fisheries) 10	**1.8**

Table 3.16. Estimated regression parameters, standard errors and t-values for the one-trend, two-explanatory factor DFA model for abundance of the 3M *Sebastes spp.* population unit, 1989–2004. **D** was explained in Chapter 2.

	Adults	Juveniles	Combined
Bottom temperature 350–500m lagged 1 year			
Estimated value from **D**	0.71	0.11	6.45
Standard error	0.48	0.16	3.00
t-value	0.52	0.16	3.34
Catch (all fisheries) lagged 10 years			
Estimated value from **D**	0.45	0.11	3.94
Standard error	0.31	0.17	-1.75
t-value	-0.29	0.17	-1.69

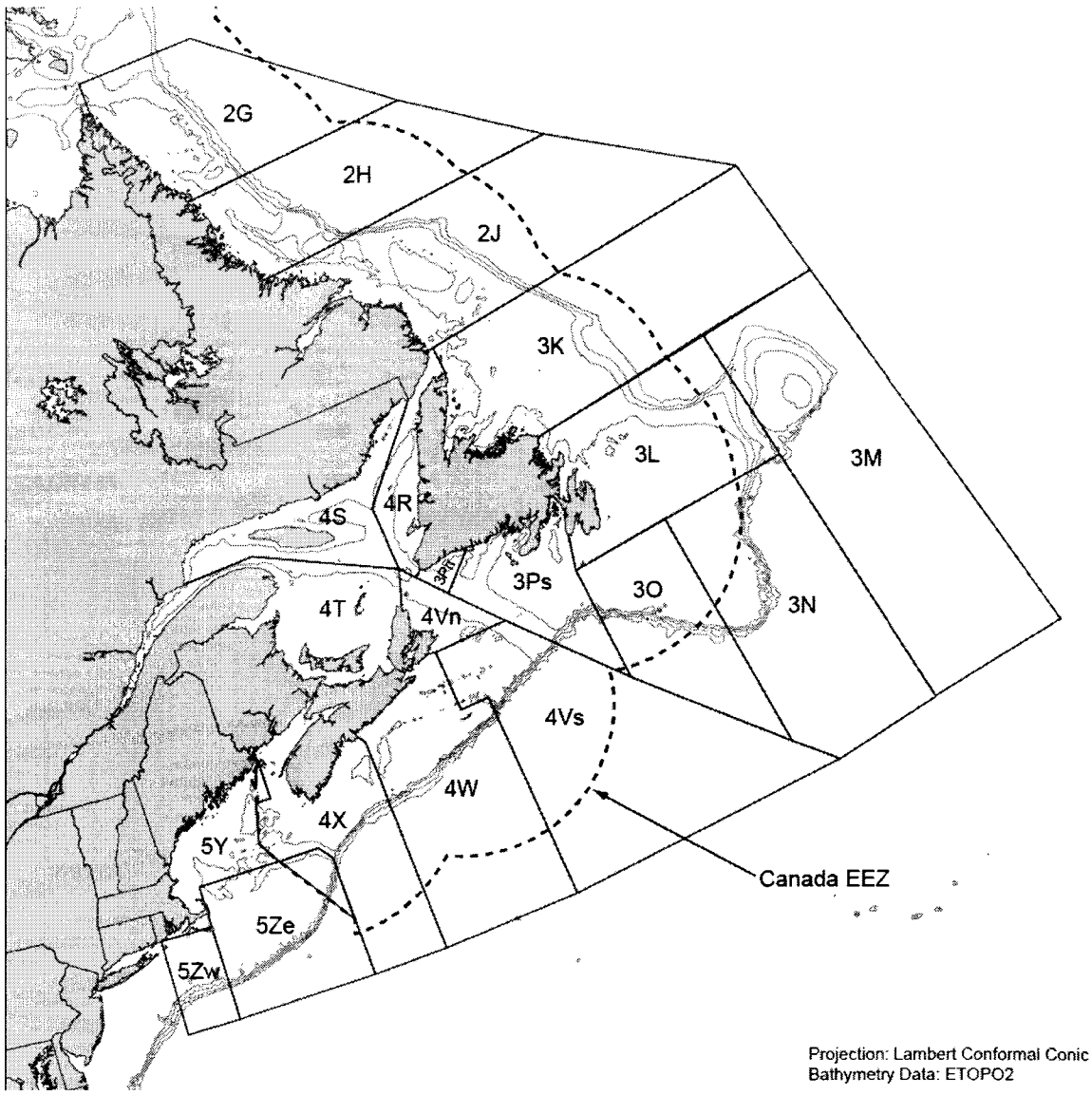

Figure 3.1. NAFO Subareas 2-5 showing Canadian economic exclusion zone (200-mile limit, dashed line) and 200, 500, 1000 and 1500 meter bathymetric contours. Map courtesy of WWF.

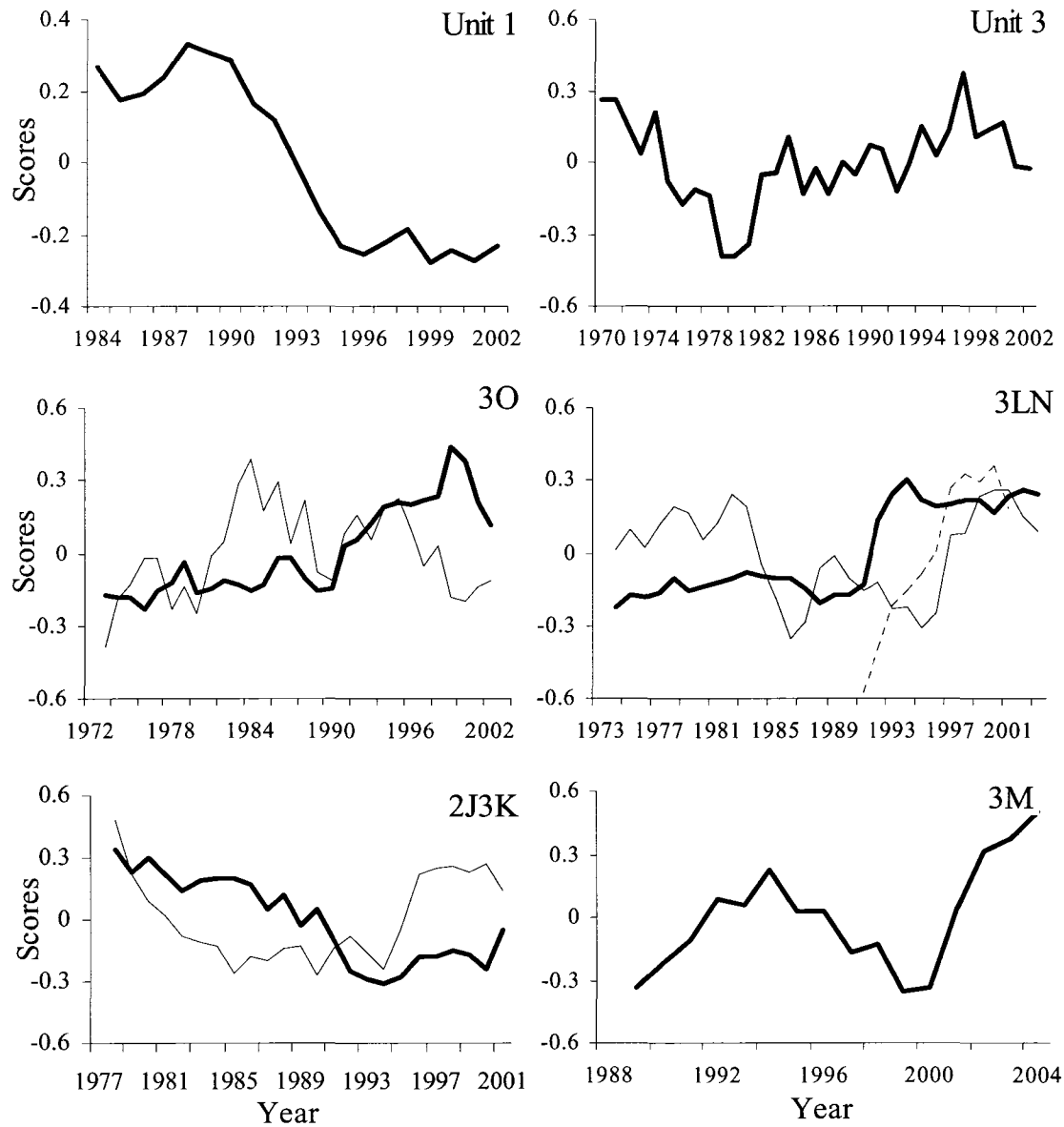

Figure 3.2. MAFA trends for the six population units of *Sebastes spp.* in the Northwest Atlantic (see text for details on units). Heavy line indicates main MAFA trend and solid light line is second trend. Not all units had two trends. 3LN stock includes abundance estimates from 2 surveys: spring survey (solid lines) and autumn survey (dotted line). Not all axes have the same scale.

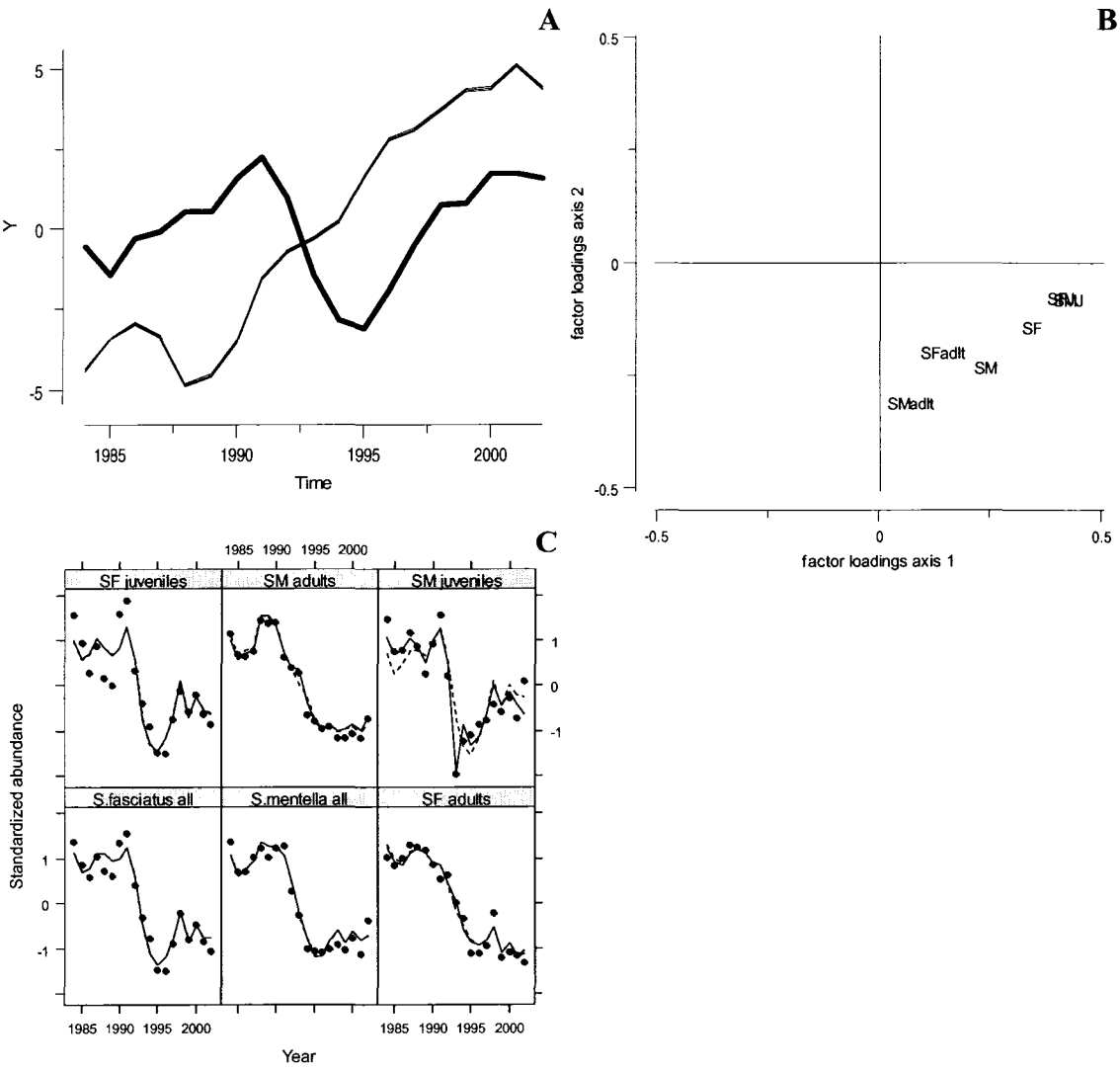

Figure 3.3. (A) Trends and confidence intervals for the two-trend, two-explanatory factors DFA model with redfish catch from the redfish fishery lagged 14 years and shrimp fishing effort lagged 9 years for abundance of the Unit 1 *Sebastes spp.* stock, 1984–2002 (main trend=heavy line); confidence intervals are plotted, but they are extremely small. (B) Plot of DFA factor loadings for combined juveniles/adults (SF, SM), juveniles (SFJ, SMJ), and adults (adlt). (C) Fit of two-trend, one-explanatory variable model (dotted) and two-trend, two-explanatory variable model (solid) to observed abundance.

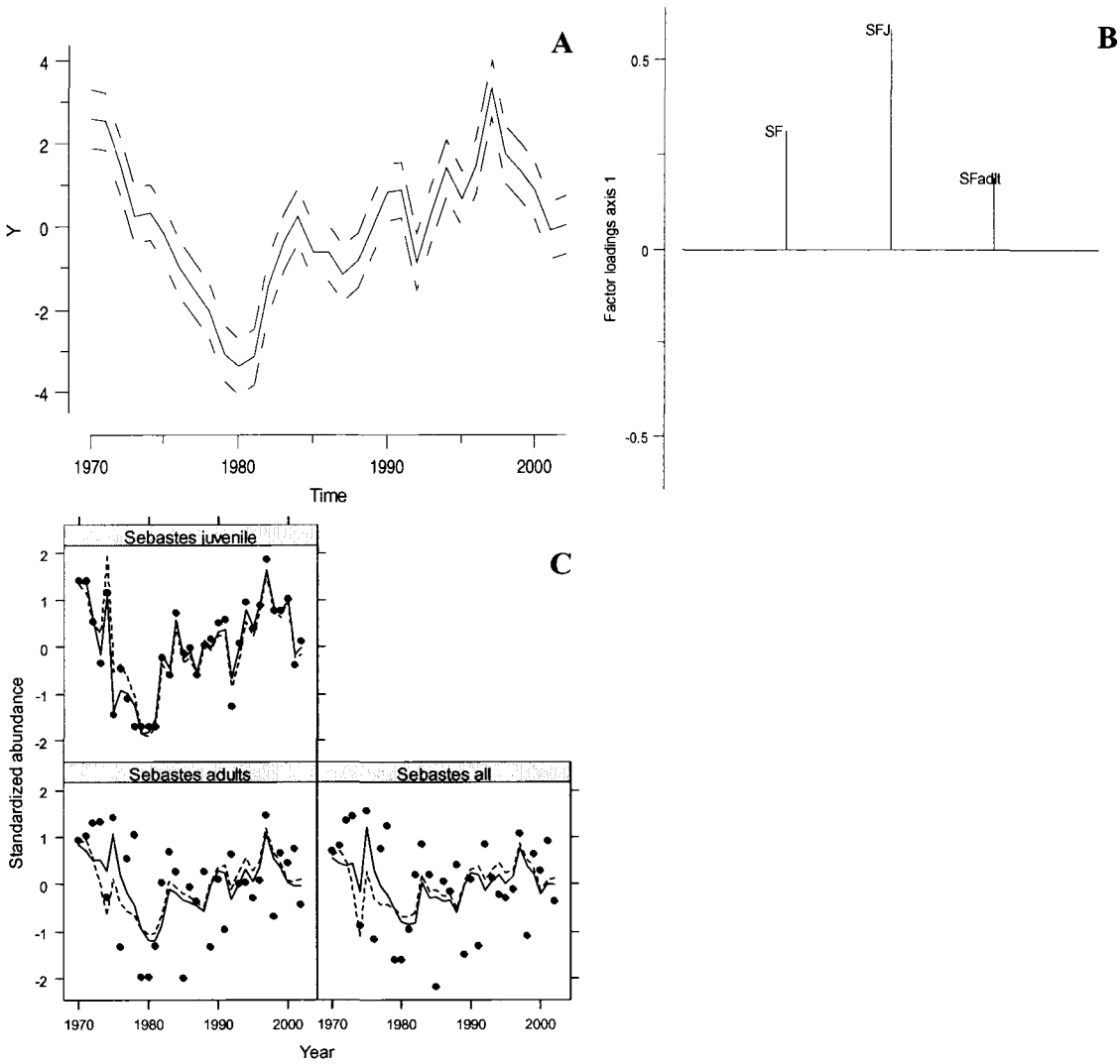

Figure 3.4. (A) Main trend and confidence interval for the DFA model with bottom temperature (350–500 m) lagged 1 year and redfish catch in all fisheries lagged 3 years for abundance of the Unit 3 *Sebastes spp.* stock, 1970–2002. (B) Plot of DFA factor loadings for combined juveniles/adults (SF), juveniles (J), and adults (adlt). (C) Fit of one-trend, one-explanatory variable model (dotted) and one-trend, two-explanatory variable model (solid) to observed abundance.

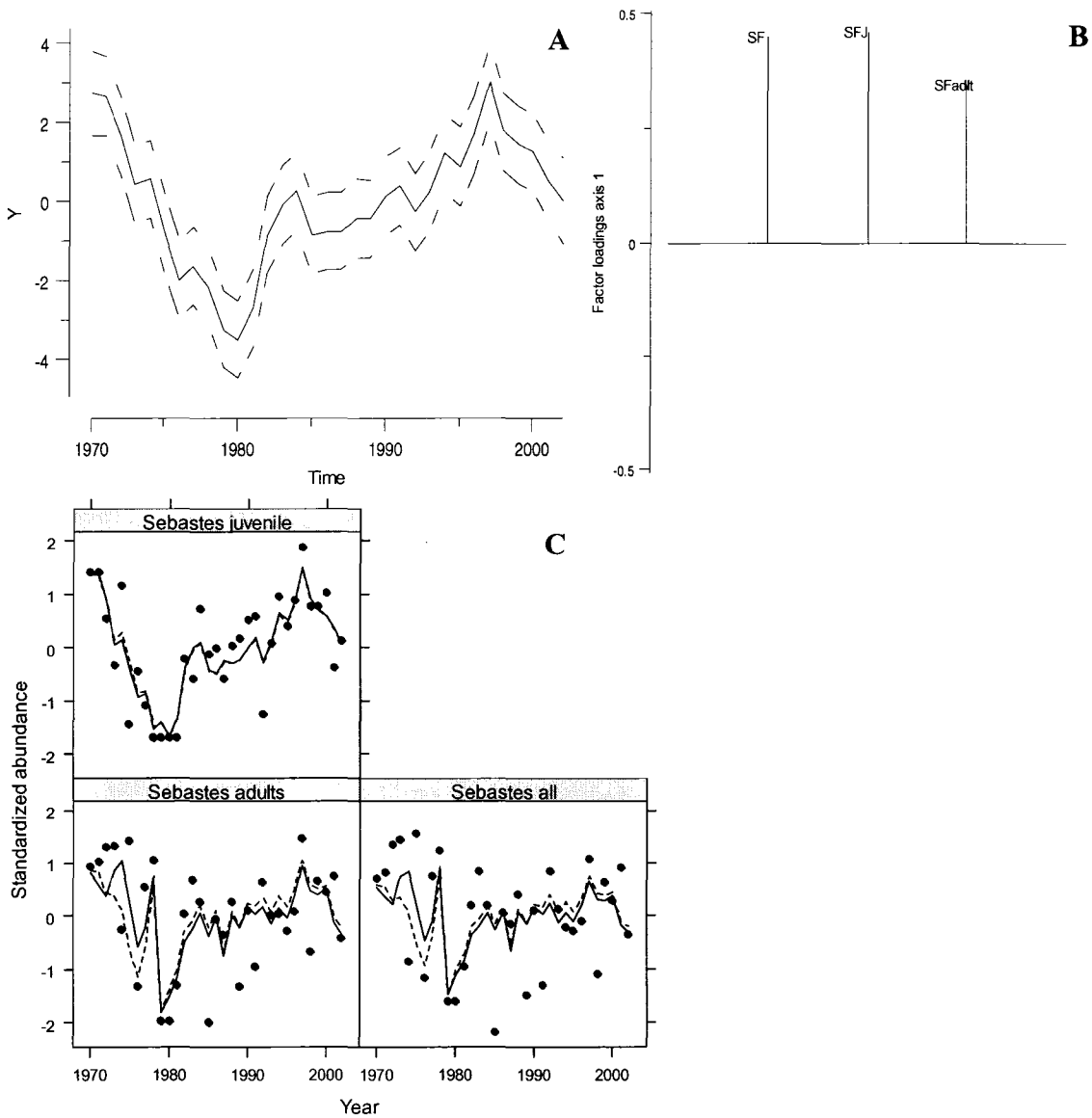

Figure 3.5. (A) Main trend and confidence intervals for the DFA model with bottom temperature (350–500 m) lagged 5 years and redfish catch from all fisheries lagged 3 years for abundance of the Unit 3 *Sebastes spp.* stock, 1970–2002. (B) Plot of DFA factor loadings for combined juveniles/adults, juveniles (J), and adults (adlt). (C) Fit of one-trend, one-explanatory variable model (dotted) and one-trend, two-explanatory variable model (solid) to observed abundance.

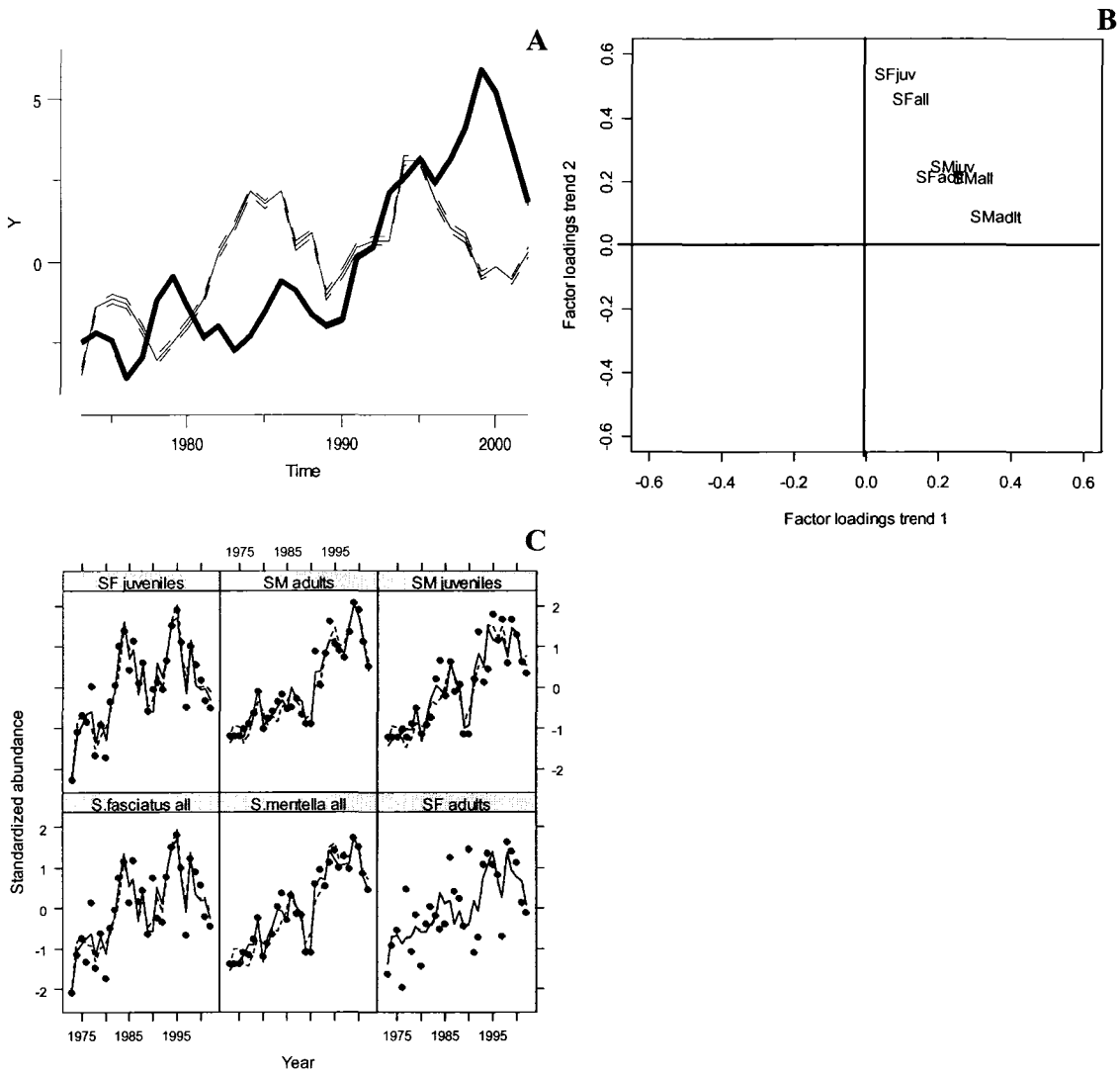

Figure 3.6. (A) The two- trend, two-explanatory variable DFA model (salinity lagged 4 years and redfish catch from all fisheries lagged 12 years) with confidence intervals for abundance of *Sebastes spp.* in NAFO Division 3O, 1973–2002 (main trend=heavy line). (B) Plot of DFA factor loadings for adults (adlt), juveniles (juv) and combined juveniles/adults (all). (C) Fit of two-trend, one-explanatory variable model (dotted) and two-trend, two-explanatory variable model (solid) to *Sebastes* abundance.

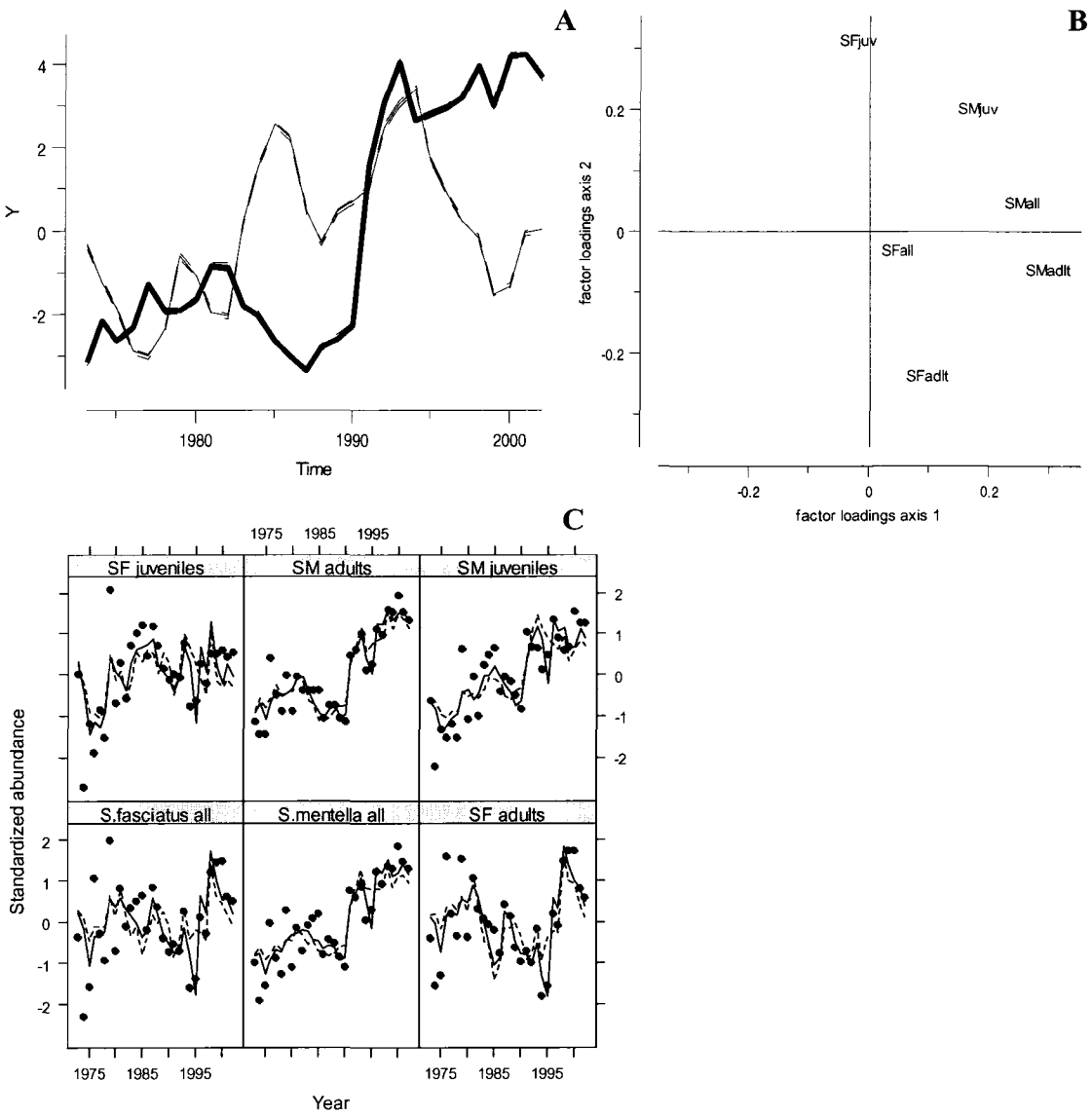

Figure 3.7. (A) The two-trend, two-explanatory variable DFA model (NAO lagged 2 years and sea surface temperature lagged 6 years) with confidence intervals for abundance of *Sebastes spp.* from spring surveys in NAFO Division 3LN, 1973–2002 (main trend=heavy line). (B) Plot of DFA factor loadings for adults (adlt), juveniles (juv), and combined juveniles/adults (all). (C) Fit of two-trend, one-explanatory variable model (dotted line) and two-trend, two-explanatory variable model (solid line) to observed abundance.

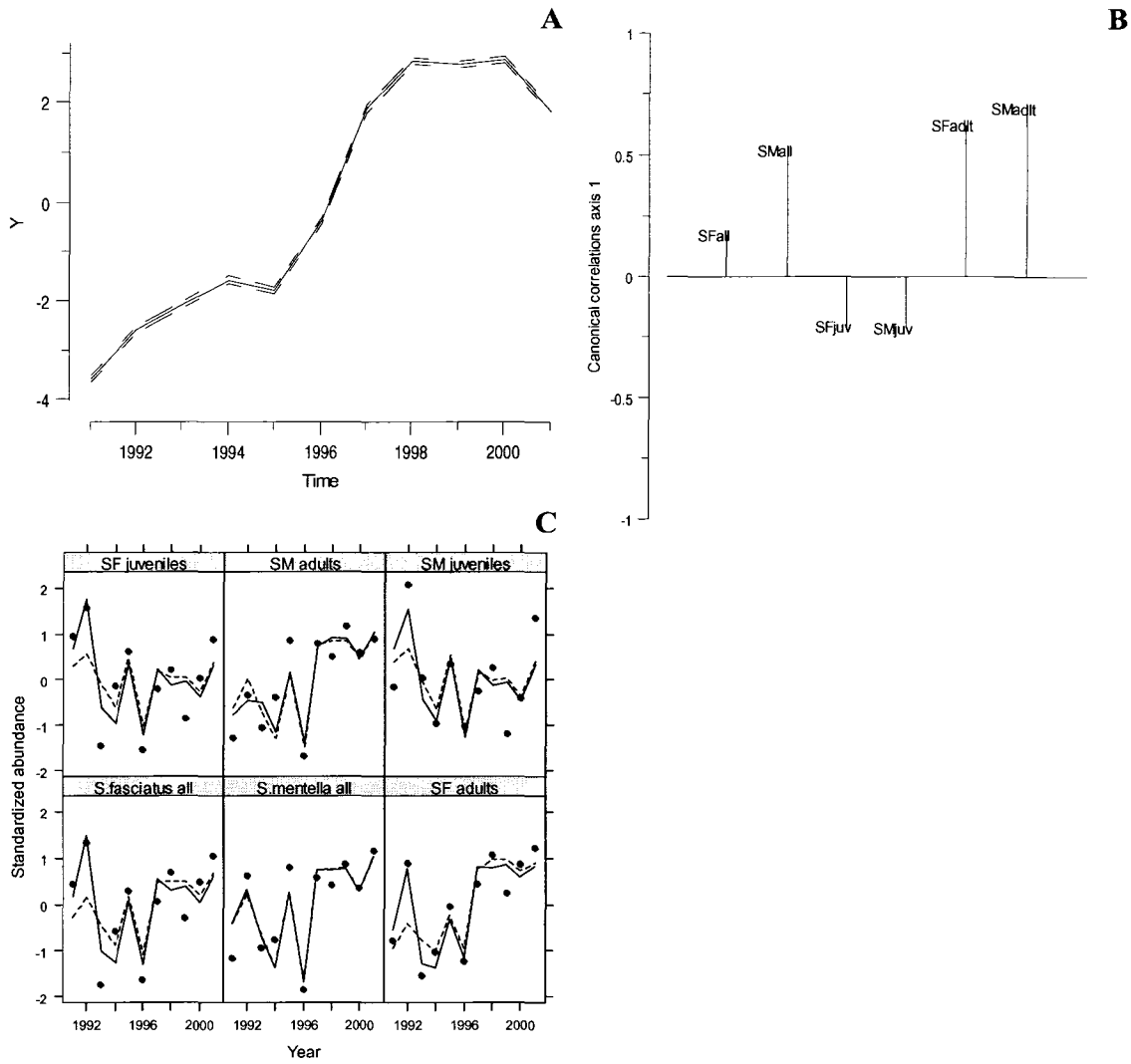

Figure 3.8. (A) The one- trend, two-explanatory variable DFA model (bottom temperature (350–500 m) lagged 7 years and sea surface temperature lagged 3 years) with confidence intervals for abundance of *Sebastes spp.* from autumn surveys in NAFO Division 3LN, 1991–2001. (B) Plot of DFA factor loadings for combined juveniles/adults (all), juveniles (juv), and adults (adlt). (C) Fit of one-trend, one-explanatory variable model (dotted line) and one-trend, two-explanatory variable model (solid line) to observed abundance.

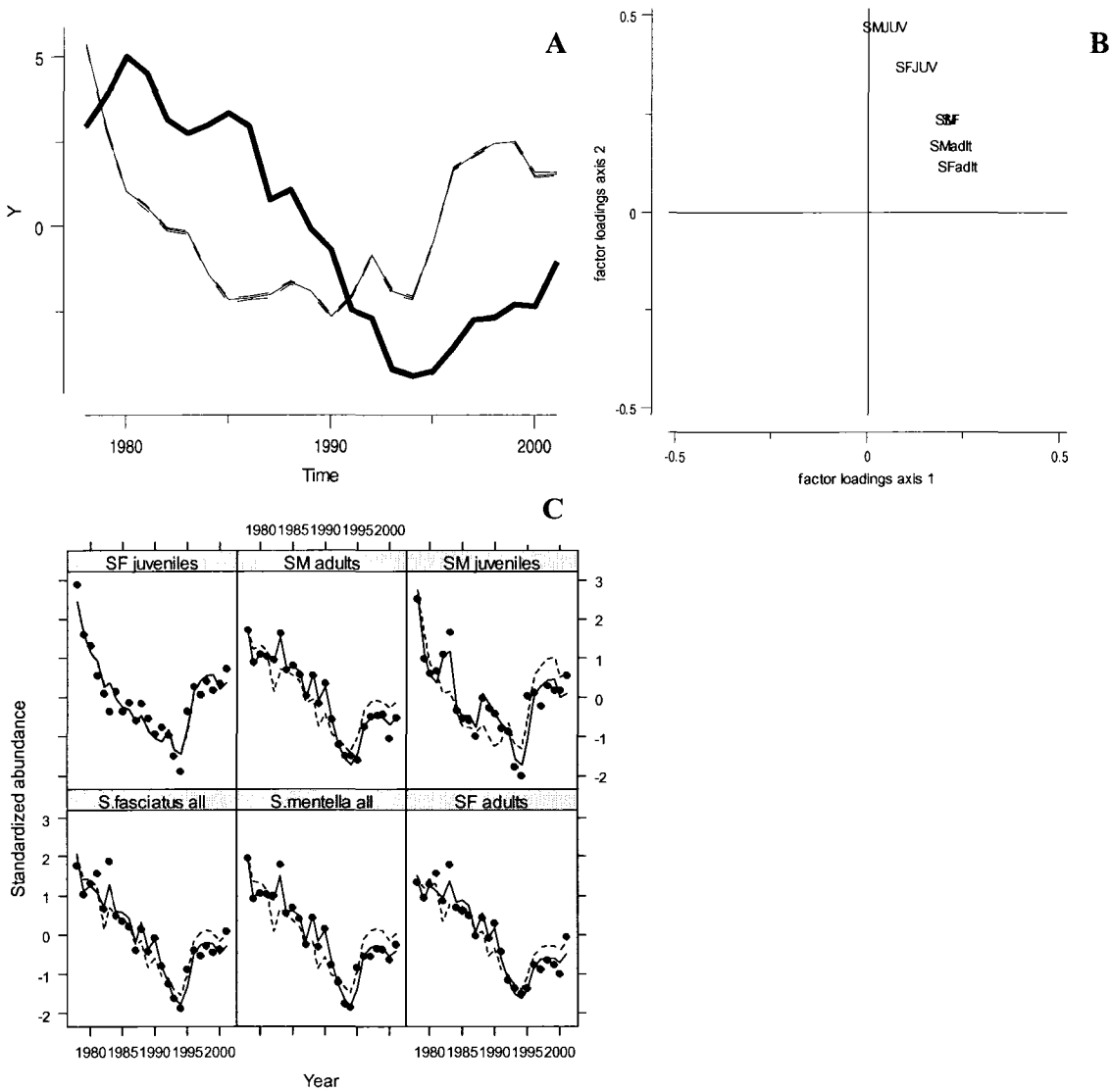

Figure 3.9. (A) The two-trend, two-explanatory variable DFA model (sea surface temperature lagged 6 years and redfish catch from the redfish fishery lagged 4 years) with confidence intervals for abundance of *Sebastes spp.* in NAFO Division 2J3K, 1978–2001 (main trend=heavy line). (B) Plot of DFA factor loadings for adults (adlt), juveniles (juv), and combined juveniles/adults. (C) Fit of two-trend, one-explanatory variable model (dotted line) and two-trend, two-explanatory variable model (solid line) to observed abundance.

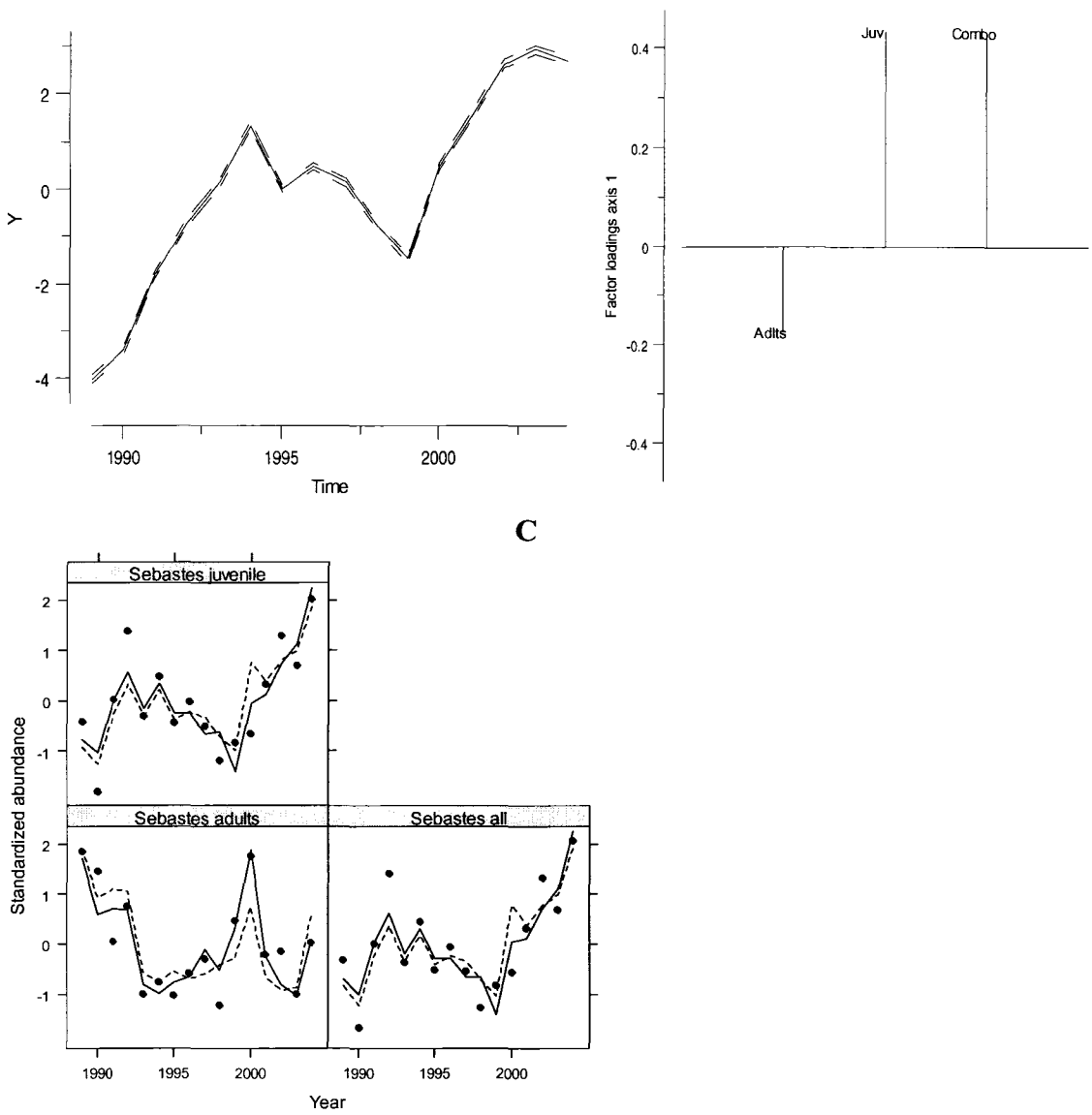

Figure 3.10. (A) Main trend and confidence intervals for the DFA model with bottom temperature (350–500 m) lagged 1 year and redfish catch from all fisheries lagged 10 years for abundance of *Sebastes spp.* in NAFO Division 3M, 1989–2004. (B) Plot of DFA factor loadings for adults (adlts), juveniles (juv), and combined juveniles/adults (combo). (C) Fit of one-trend, one-explanatory variable model (dotted) and one-trend, two-explanatory variable model (solid) to observed abundance.

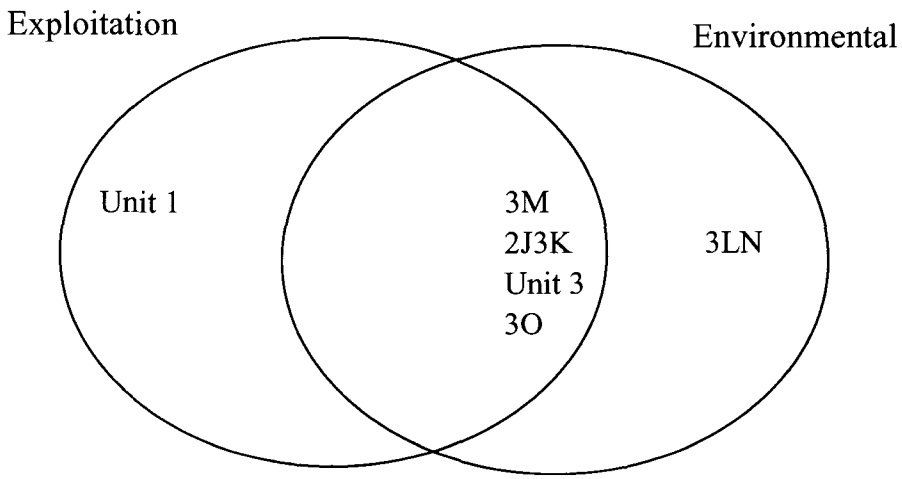

Figure 3.11. Main factors found to improve the two-variable DFA model for each population unit.

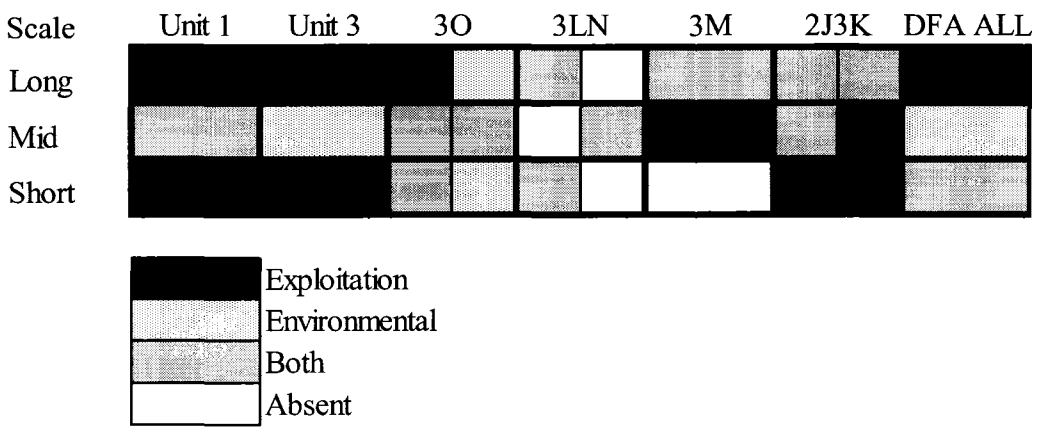

Figure 3.12. Temporal scale on which environmental and exploitation factors operate for each population unit as estimated by MAFA; ALL summarizes the results of DFA. Populations 3O, 3LN and 2J3K each had two trends estimated by MAFA and factors related to each trend are shown separately. Non-stippled sections indicate no factor was important at that scale.

Appendix A.

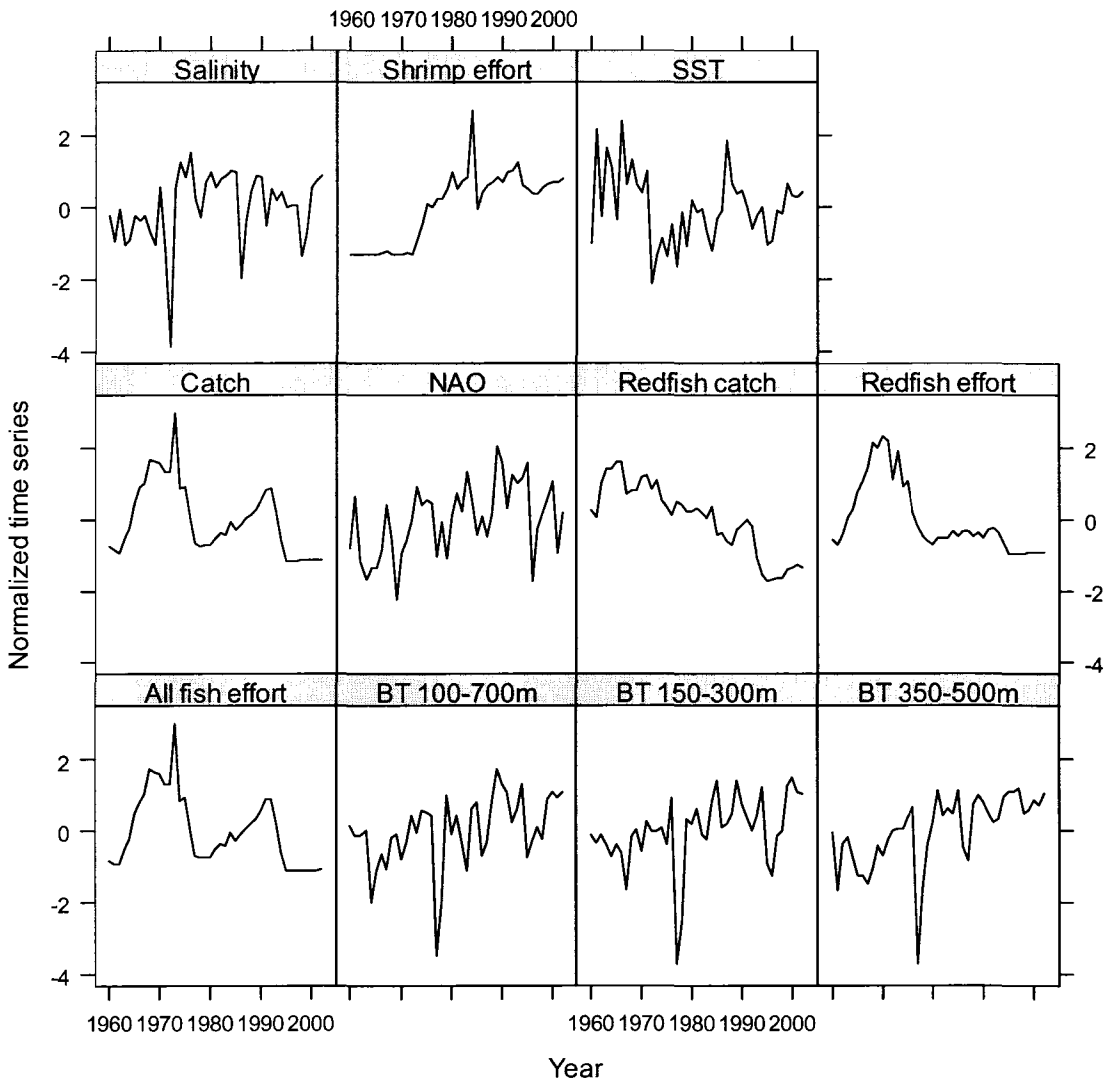

Figure 1A. Standardized explanatory variables from the Northern Gulf of St. Lawrence, 1960–2002; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

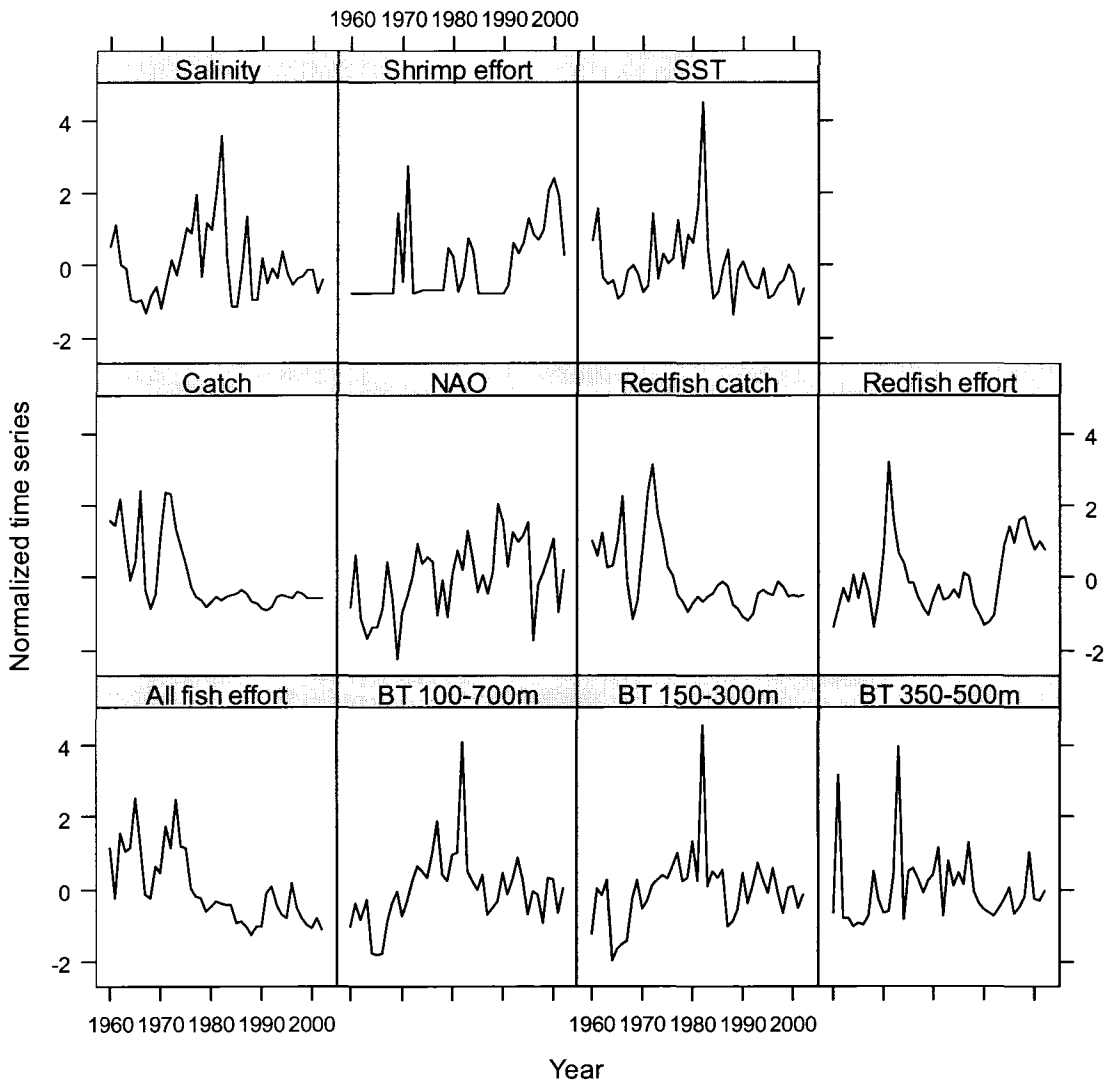

Figure 2A. Standardized explanatory variables from the Scotian Shelf, 1960–2002; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

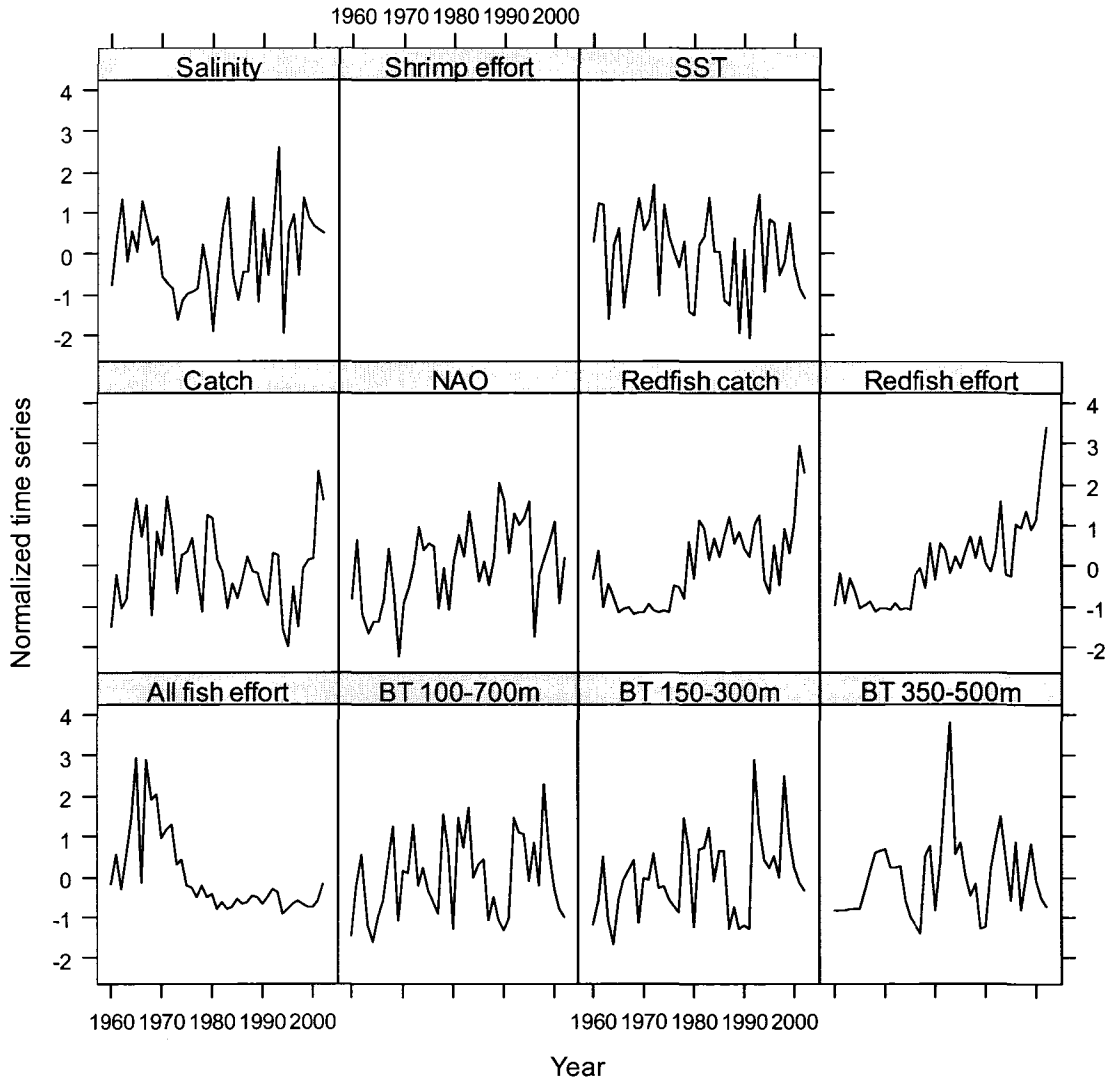

Figure 3A. Standardized explanatory variables from NAFO Division 3O, 1960–2002; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

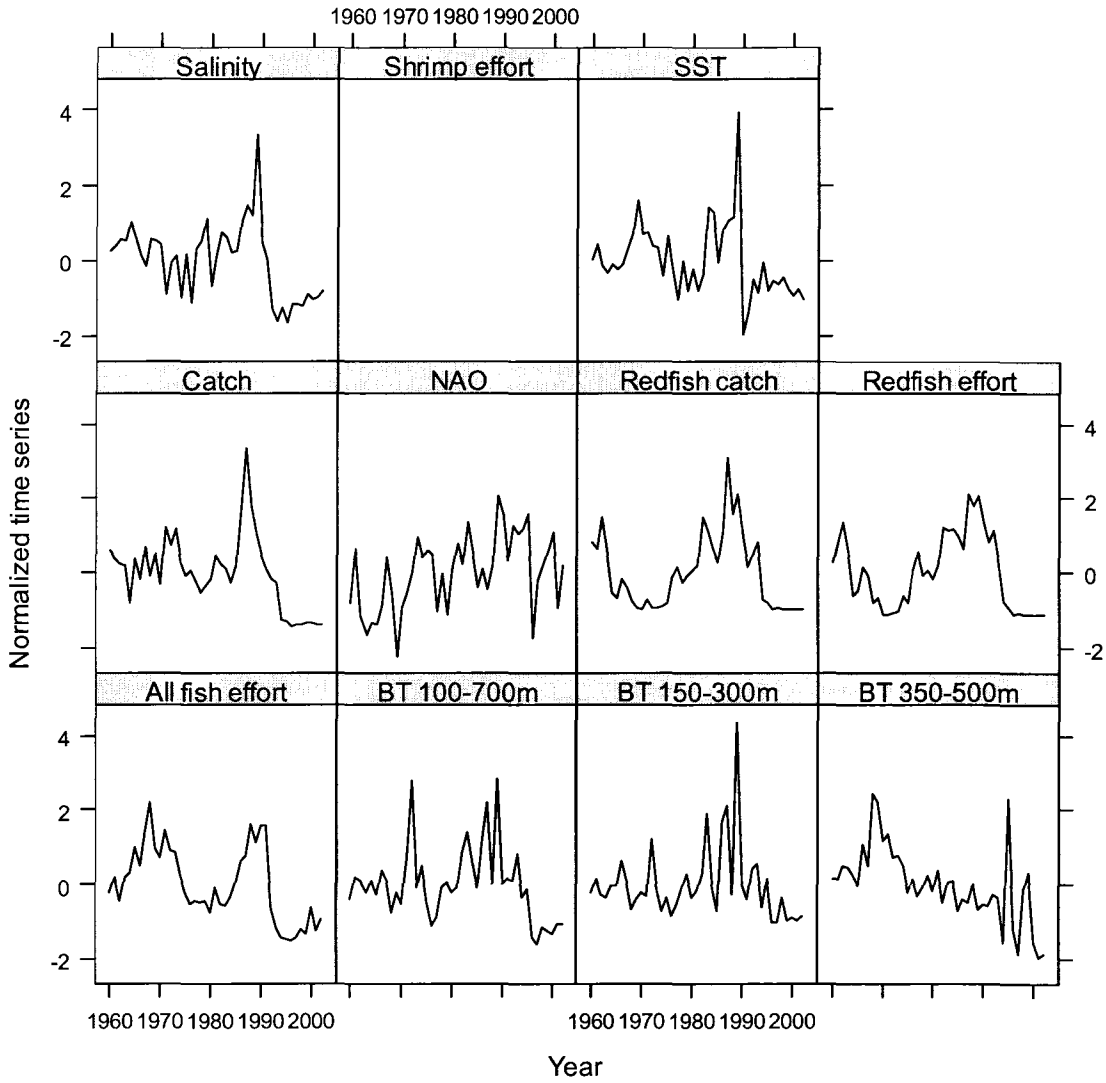

Figure 4A. Standardized explanatory variables from the NAFO Divisions 3LN, 1960–2002; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

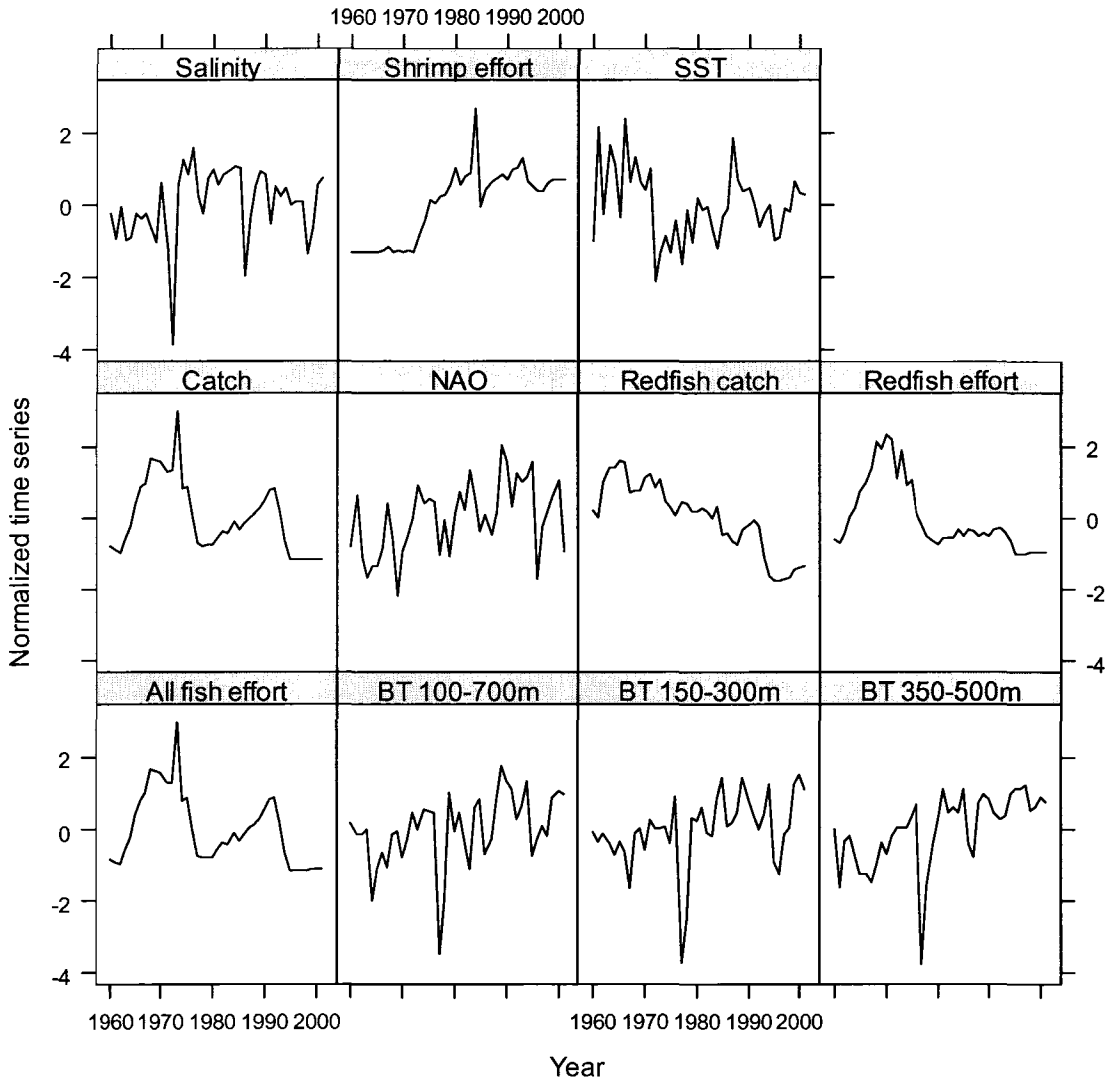

Figure 5A. Standardized explanatory variables from the NAFO Divisions 2J3K, 1960–2001; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

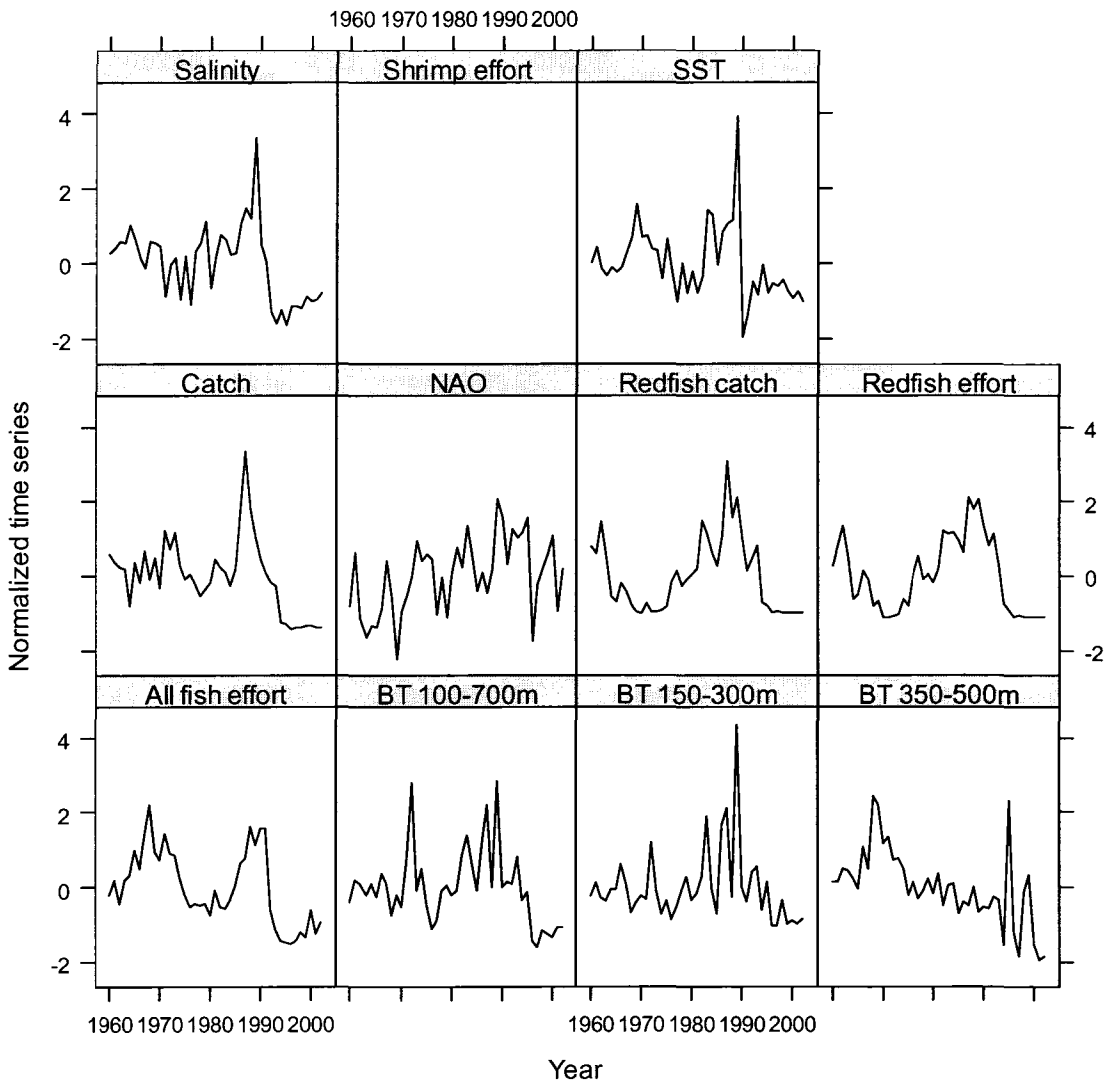

Figure 6A. Standardized explanatory variables from the NAFO Division 3M, 1960–2004; SST = sea surface temperature, BT = bottom temperature, NAO is the North Atlantic Oscillation winter index, all fish effort and catch are from all fisheries catching redfish.

Appendix B.

Table 1B. Time series of explanatory variables used for redfish *Sebastes spp.* population Unit 1, 1960–2002.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	3.9	4.8	3.7	2.5	32.3	0	1469	9907	16489	12219
1961	3.7	4.1	3.5	4.9	32.0	0	1066	7060	14803	10366
1962	3.9	4.7	3.5	3.1	32.4	0	2112	5755	22749	6759
1963	3.7	4.7	3.6	4.5	32.0	0	3840	19386	26085	20440
1964	3.5	4.5	2.4	4.1	32.0	0	4729	28849	26013	30301
1965	3.7	4.2	2.9	3.0	32.3	0	6525	50393	27644	52339
1966	3.5	4.2	3.2	5.1	32.2	150	7589	61497	27489	67298
1967	2.9	4.1	3.0	3.8	32.3	441	8929	69075	20327	70197
1968	3.9	4.4	3.5	4.3	32.1	0	11615	89877	20983	92302
1969	4.0	4.6	3.6	3.8	32.0	96	11027	87690	21059	90837
1970	3.6	4.5	3.1	3.6	32.6	13	12348	86577	24011	89284
1971	4.1	4.7	3.4	4.0	31.9	228	11821	77683	24477	80413
1972	4.0	4.8	3.8	1.7	30.8	54	7839	77174	21540	81598
1973	4.0	4.9	3.6	2.3	32.6	1530	10781	131013	23413	133848
1974	4.0	4.8	3.9	2.6	32.9	3082	7151	62204	18605	65576
1975	3.7	5.0	3.9	2.3	32.8	5060	7639	64865	17258	67346
1976	4.6	5.1	3.8	2.9	33.1	4746	4284	36706	15127	39166
1977	1.4	3.1	1.5	2.0	32.5	5492	2951	13732	18273	15401
1978	2.2	4.1	2.4	3.2	32.3	5545	1854	11761	17684	13269
1979	4.2	4.7	4.2	2.5	32.7	6551	1369	11877	16141	14131
1980	4.1	4.9	3.5	3.4	32.8	8183	961	12584	16128	13785
1981	4.4	5.4	3.9	3.1	32.6	6578	1642	19756	16678	20326
1982	3.9	5.0	3.4	3.2	32.7	7373	1705	24491	15796	25642
1983	3.8	5.1	2.9	2.7	32.8	7691	1735	23232	14543	24103
1984	4.5	5.0	3.9	2.3	32.8	14253	2493	33858	17182	35108
1985	4.9	5.3	4.1	3.0	32.8	4524	1817	26847	10556	27441
1986	4.0	4.6	3.2	3.2	31.6	6102	2441	32753	10957	33302
1987	4.1	4.5	3.4	4.7	32.2	6870	2375	37760	9082	38319
1988	4.3	5.2	4.1	3.8	32.6	7206	1823	41363	8560	41999
1989	4.9	5.3	4.6	3.5	32.8	7667	2215	45980	11872	46642
1990	4.5	5.2	4.4	3.6	32.8	7143	1793	54251	12950	55245
1991	4.2	5.0	4.2	3.3	32.2	8110	2526	63303	14152	64276
1992	3.9	4.9	3.7	2.8	32.6	8329	2698	64602	12725	65468
1993	4.2	5.0	4.0	3.1	32.5	9231	2177	43210	5309	43581
1994	4.8	5.3	4.4	3.3	32.6	6885	1267	16711	1365	16741
1995	3.3	5.3	3.2	2.5	32.4	6506	0	8	80	43
1996	3.1	5.3	3.4	2.6	32.4	5963	2	26	178	43
1997	3.9	5.4	3.7	3.2	32.4	5982	2	8	649	20
1998	4.0	5.1	3.5	3.1	31.8	6702	51	330	734	341
1999	4.8	5.1	4.1	3.8	32.1	7032	156	1031	2685	1042
2000	5.0	5.2	4.2	3.5	32.6	7158	159	1046	3011	1056
2001	4.7	5.2	4.1	3.5	32.7	7147	157	1153	3578	1158
2002	4.7	5.3	4.2	3.6	32.8	7420	196	1197	2967	1211

Table 2B. Time series of explanatory variables used for redfish *Sebastes spp.* population Unit 3, 1960–2002.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	6.4	5.0	5.7	10.0	33.8	0	206	11217	12224	23470
1961	8.3	11.7	6.8	12.3	34.2	0	429	9404	6113	22341
1962	8.0	4.8	6.0	7.3	33.5	0	642	12045	14158	28981
1963	8.6	4.7	6.9	6.8	33.5	0	484	7926	11738	17365
1964	5.2	4.3	4.6	7.0	32.9	0	797	8082	12342	8927
1965	5.7	4.5	4.5	5.7	32.9	0	531	11059	18312	13317
1966	5.9	4.4	4.6	6.0	33.0	0	813	16492	12449	30733
1967	6.1	4.8	5.9	7.8	32.7	0	597	6025	6425	6557
1968	7.8	7.0	6.8	8.1	33.0	0	200	1752	6102	1997
1969	8.6	5.6	7.3	7.6	33.2	335	531	3967	10018	5789
1970	7.4	5.0	6.2	6.2	32.8	47	1098	10138	9221	19460
1971	7.8	5.1	6.8	6.7	33.2	533	2114	16960	14939	30427
1972	8.4	6.9	7.7	11.9	33.6	0	1444	20253	12154	30058
1973	8.6	13.1	8.4	7.2	33.4	7	1051	14397	18278	21516
1974	8.8	4.7	8.2	9.0	33.7	8	937	11481	12378	16960
1975	8.7	7.1	7.9	8.2	34.1	12	696	8018	12282	12465
1976	9.2	7.2	9.0	8.7	34.0	14	703	6948	7214	7459
1977	9.7	6.6	10.3	11.5	34.6	8	529	4465	6301	4901
1978	8.6	6.0	8.0	7.9	33.3	9	404	3697	6039	3955
1979	8.7	6.5	7.7	10.3	34.2	186	330	2437	4335	2621
1980	10.2	6.8	8.9	9.8	34.1	152	526	3621	5030	3858
1981	8.5	8.1	9.0	12.5	34.7	4	688	4331	5654	4702
1982	15.3	4.8	13.9	20.0	35.6	70	512	3789	5403	4130
1983	8.3	7.5	8.1	9.3	33.6	228	530	4281	5349	4821
1984	9.0	6.3	7.8	5.7	32.8	174	626	4786	5251	5151
1985	8.7	7.0	7.4	6.1	32.8	0	537	5723	2901	5819
1986	9.0	6.3	8.0	8.0	33.5	0	825	6156	3189	6409
1987	6.6	8.4	6.2	9.3	34.3	0	775	5571	2487	5877
1988	6.8	6.1	6.6	4.5	33.0	0	458	3340	1601	3502
1989	7.3	5.4	6.8	7.8	32.9	0	352	3005	2662	3122
1990	8.9	5.1	8.1	8.3	33.6	0	228	1828	2492	1991
1991	7.6	5.0	7.1	7.3	33.2	30	249	1517	6759	1623
1992	8.4	4.8	7.8	6.5	33.5	209	330	2293	7449	2460
1993	9.3	5.2	8.7	6.4	33.3	169	768	4688	5291	4764
1994	8.6	5.7	7.8	7.9	33.7	209	1147	5167	4039	5237
1995	8.0	6.2	6.3	5.7	33.4	314	1359	4795	3610	4825
1996	9.1	4.9	7.3	5.9	33.2	242	1176	4479	7938	4530
1997	8.0	5.3	7.2	6.6	33.3	220	1436	6093	4889	6145
1998	7.2	5.7	5.9	7.1	33.3	264	1480	5605	3616	5642
1999	8.3	7.9	7.9	8.2	33.4	438	1261	4322	2718	4343
2000	8.4	5.6	7.8	7.6	33.4	481	1083	4562	2400	4591
2001	7.4	5.6	6.4	5.2	33.0	403	1187	4288	3591	4312
2002	8.0	6.1	7.4	6.5	33.3	159	1083	4625	2111	4674

Table 3B. Time series of explanatory variables used for redfish *Sebastes spp.* population 3O, 1960–2002.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	3.7	3.9	3.0	7.9	33.4	N/A	53	4699	2671	4984
1961	4.8	3.9	4.8	9.9	33.9		314	8599	4707	10805
1962	7.0	3.9	6.1	9.8	34.3		65	863	2279	7172
1963	3.8	3.9	3.4	4.1	33.6		276	3901	4768	8284
1964	2.7	3.9	2.7	7.8	34.0		162	2167	7253	15439
1965	4.9	3.9	3.7	8.6	33.7		22	237	11611	19654
1966	5.9	4.3	4.3	4.7	34.3		50	521	2755	15235
1967	6.4	4.7	5.7	6.7	34.1		83	852	11512	18780
1968	6.9	5.0	7.2	8.7	33.8		1	2	8593	6385
1969	3.8	5.0	3.6	10.1	33.9		25	135	8942	15841
1970	5.9	5.1	5.4	8.5	33.5		22	229	5918	13155
1971	5.9	4.7	5.4	9.1	33.4		11	1233	6557	19738
1972	7.2	4.7	7.2	10.8	33.3		64	408	6922	15951
1973	5.5	4.8	4.9	5.3	32.9		19	86	4092	8752
1974	5.6	4.1	5.6	9.8	33.2		32	304	4368	13083
1975	4.9	3.8	4.7	8.2	33.3		14	101	2452	13553
1976	4.6	3.6	4.2	7.5	33.3		300	3661	2329	15023
1977	4.3	3.5	3.8	6.7	33.3		353	3441	1657	10782
1978	8.9	5.0	7.6	8.0	33.8		188	2054	2505	6727
1979	7.4	5.1	6.2	4.5	33.5		569	9572	1671	17693
1980	3.5	3.9	3.2	4.3	32.8		263	4625	1875	17304
1981	7.4	4.9	7.5	7.8	33.5		557	12603	802	12603
1982	7.4	6.2	6.4	8.2	34.0		505	11335	1316	11348
1983	8.5	7.5	7.9	10.2	34.3		320	7133	871	7140
1984	5.8	5.0	5.2	7.4	33.5		451	9993	927	10022
1985	7.3	5.2	5.7	7.5	33.2		361	7567	1607	8198
1986	7.3	4.6	5.9	5.0	33.5		497	10403	1243	10409
1987	3.4	4.2	3.5	4.8	33.5		615	12970	1375	12985
1988	4.5	4.4	4.4	8.1	34.4		443	9398	1787	11286
1989	3.4	3.6	3.6	3.4	33.2		613	11017	1731	11043
1990	3.6	3.6	3.2	7.5	34.0		402	8753	1247	8860
1991	3.4	4.7	3.6	3.1	33.5		331	7533	1619	7549
1992	11.8	5.2	7.5	8.6	34.1		499	11821	2209	13303
1993	8.5	5.7	6.9	10.3	34.9		901	13146	2066	13159
1994	6.9	4.9	6.9	5.4	32.8		309	4556	444	4582
1995	6.4	4.1	5.1	9.0	34.0		292	2723	820	2814
1996	7.1	5.2	6.5	8.9	34.2		715	9298	1232	9643
1997	6.0	3.9	4.9	6.3	33.5		682	3708	1408	4984
1998	11.1	4.5	8.8	7.0	34.4		826	11460	1186	11579
1999	8.0	5.2	6.2	8.9	34.1		675	8044	1020	12593
2000	8.0	5.2	6.2	8.9	34.1		757	12261	930	12789
2001	8.0	5.2	6.2	8.9	34.1		1168	22574	1447	22574
2002	8.0	5.2	6.2	8.9	34.1		1512	18792	2654	19446

Table 4B. Time series of explanatory variables used for redfish *Sebastes spp.* population 3LN, 1960–2002.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	1.6	3.6	2.0	5.0	33.4	N/A	575	14581	7663	26111
1961	2.0	3.6	2.5	5.7	33.5		812	13162	9988	22856
1962	1.5	3.8	2.5	4.7	33.6		1016	20102	6226	21105
1963	1.4	3.8	2.2	4.4	33.6		687	12509	9765	20727
1964	1.8	3.6	2.5	4.8	33.8		204	3764	10647	7756
1965	1.8	3.4	2.1	4.6	33.6		273	2731	14472	22847
1966	2.5	4.3	2.7	4.8	33.3		529	6383	11587	16160
1967	1.9	3.9	2.5	5.5	33.2		428	4613	16806	26851
1968	1.1	5.3	1.7	6.2	33.6		131	1711	21597	17325
1969	1.4	5.1	2.2	7.6	33.6		181	509	14299	24544
1970	1.6	4.3	1.9	6.1	33.5		2	81	12942	14172
1971	1.5	4.5	3.0	6.2	32.8		8	2305	17270	34074
1972	3.1	4.0	5.0	5.7	33.3		24	330	14072	27684
1973	1.7	4.0	2.3	5.5	33.4		36	412	13843	33165
1974	1.0	3.8	2.8	4.3	32.8		201	786	10237	21981
1975	1.4	3.3	1.9	6.0	33.4		133	1605	7641	16923
1976	0.9	3.6	1.3	4.6	32.7		495	6953	5612	19143
1977	1.2	3.3	1.5	3.2	33.4		683	9214	6241	15364
1978	1.7	3.4	2.3	4.9	33.6		432	5690	6065	11522
1979	2.1	3.7	2.4	3.6	33.9		481	7217	6119	13916
1980	1.4	3.3	2.2	4.6	33.0		399	8422	4360	15980
1981	1.6	3.7	2.3	3.6	33.4		539	9364	8369	24057
1982	2.1	3.1	3.2	4.3	33.7		969	20137	5706	21438
1983	3.9	3.5	3.7	7.4	33.6		929	17104	5574	19538
1984	1.8	3.5	3.0	7.1	33.4		951	13275	6665	14674
1985	1.0	2.9	2.3	4.8	33.4		857	10248	9234	20444
1986	3.6	3.2	3.5	6.4	33.8		734	16870	12619	41741
1987	4.1	3.1	4.4	6.7	34.1		1341	33032	13391	61574
1988	1.5	3.5	2.4	6.9	33.9		1208	20891	18094	41667
1989	6.6	3.0	5.0	11.6	35.0		1317	25041	15409	31502
1990	1.8	3.1	2.4	1.6	33.5		1017	16369	17876	24162
1991	1.4	3.0	2.5	2.6	33.3		804	8962	18030	19308
1992	2.3	3.3	2.5	4.1	32.6		926	12198	5098	15812
1993	2.4	3.2	3.1	3.5	32.5		575	14600	2119	14862
1994	1.1	2.3	2.0	4.9	32.6		153	2298	507	2300
1995	2.0	5.2	2.3	3.6	32.4		70	1422	158	1622
1996	0.7	2.6	1.0	4.0	32.7		3	34	106	37
1997	0.7	2.1	0.9	3.9	32.7		21	395	543	498
1998	1.4	3.4	1.3	4.2	32.7		0	0	1762	143
1999	0.7	3.7	1.2	3.7	32.8		1	5	956	953
2000	0.8	2.3	1.1	3.3	32.8		0	0	5089	965
2001	0.7	2.0	1.4	3.7	32.8		2	17	1483	552
2002	0.9	2.1	1.4	3.2	32.9		0	0	3393	294

Table 5B. Time series of explanatory variables used for redfish *Sebastes spp.* population 2J3K, 1960–2001.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	1.7	3.7	2.8	4.6	33.2	0	996	17444	26266	126034
1961	2.2	3.1	2.6	4.8	33.5	0	3752	20078	19195	55455
1962	1.7	3.3	2.4	2.7	33.8	0	161	4715	10014	19657
1963	2.9	3.6	3.0	4.0	34.0	0	174	10152	4405	23644
1964	1.7	3.7	2.7	3.8	34.2	0	63	16122	1621	50154
1965	2.1	4.1	2.8	3.7	33.8	0	97	18010	2141	43539
1966	3.7	4.1	3.9	5.0	34.5	0	1821	17167	14081	32730
1967	1.7	3.9	2.5	3.3	34.1	0	80	16347	1937	26154
1968	2.1	3.6	2.9	4.4	34.3	0	111	21844	1029	18866
1969	2.1	3.5	2.9	4.1	34.1	0	0	20539	0	24566
1970	2.4	4.2	3.5	3.3	34.1	0	0	14961	0	21797
1971	2.6	3.8	3.2	3.3	34.1	0	12	14131	247	19290
1972	2.1	3.3	2.6	2.1	33.8	0	6	15825	300	19402
1973	1.6	3.2	2.4	3.8	33.5	0	43	16767	235	38898
1974	1.9	3.4	2.4	3.0	33.6	2	483	17979	6385	30134
1975	1.4	3.0	1.9	2.9	33.4	3	50	20601	373	24854
1976	2.1	3.1	2.7	5.9	33.9	99	279	8618	3859	24628
1977	1.9	3.3	2.5	2.4	33.6	295	404	7757	4666	16521
1978	2.0	3.2	2.6	2.1	33.9	298	1612	8909	22792	28118
1979	2.1	3.4	2.8	2.2	33.5	479	1186	7308	23539	30433
1980	1.4	3.1	2.0	2.6	33.5	515	652	6150	9990	14015
1981	1.7	3.2	2.5	2.5	33.5	487	753	8444	12175	16517
1982	1.7	3.1	2.4	2.8	33.5	542	606	4052	12580	17658
1983	4.6	3.3	4.4	4.6	33.1	206	438	3724	9923	14134
1984	3.0	3.2	3.0	1.6	33.9	162	952	3687	19915	23273
1985	2.9	3.4	3.0	2.5	34.1	401	1099	4108	20303	29067
1986	2.8	2.8	2.8	4.0	34.2	265	1152	4619	20625	26020
1987	2.5	3.3	2.6	2.1	32.2	647	1044	6278	14909	17428
1988	2.0	3.3	2.6	2.4	33.8	1354	391	6135	5330	6824
1989	1.6	3.0	2.4	1.9	33.2	1786	148	6454	2059	3065
1990	2.3	2.7	2.6	1.1	34.2	1488	150	5011	1797	2306
1991	1.2	3.3	2.5	1.5	31.6	1867	32	2858	101	235
1992	1.9	2.9	2.6	1.7	33.7	1946	5	128	6	15
1993	1.9	3.3	2.9	2.4	33.7	1922	0	36	0	0
1994	1.5	2.6	2.4	2.4	33.4	2020	0	1	0	0
1995	1.8	3.0	2.3	3.2	33.6	1762	0	0	0	1
1996	1.6	2.8	2.2	3.6	33.2	1586	0	33	0	0
1997	2.4	3.2	2.8	3.7	33.6	3997	0	41	0	0
1998	2.1	3.4	2.8	3.7	33.7	7848	0	177	0	0
1999	2.2	3.5	2.9	3.8	33.5	8707	1	216	2	3
2000	1.9	3.6	3.0	2.8	33.6	8822	0	170	0	5
2001	2.0	3.4	2.8	3.5	33.7	7064	83	179	1522	1524

Table 6B. Time series of explanatory variables used for redfish *Sebastes spp.* population 3M, 1960–2004.

Year	150–300 BT	350–500 BT	100–700 BT	SST	SAL	SHEFF	REDEFF	REDCT	FISHEFF	CT
1960	3.7	3.6	4.0	6.4	34.5	N/A	10	135	2553	8419
1961	3.6	3.8	3.7	6.4	34.5		2731	11287	3680	15714
1962	3.9	3.7	3.8	6.6	34.6		4	32	239	6958
1963	3.9	3.7	3.9	6.2	34.6		0	0	2580	7025
1964	3.8	3.8	3.8	6.7	34.7		135	1015	7151	13983
1965	4.9	3.7	4.2	7.0	34.6		6	79	9715	29840
1966	4.2	4.9	4.1	6.6	34.6		3282	6966	4118	7241
1967	5.7	3.9	4.7	8.4	34.7		0	0	1299	729
1968	4.5	4.0	4.2	6.9	34.5		0	0	2476	4763
1969	4.0	3.8	3.9	9.0	34.6		602	2015	1462	2485
1970	4.6	4.0	4.4	8.2	34.3		0	0	1481	3168
1971	5.0	4.2	4.9	8.3	34.8		0	1778	1945	8033
1972	6.0	6.7	6.1	11.3	34.7		6	177	5360	40173
1973	4.5	6.7	5.0	7.8	34.2		39	773	2499	22288
1974	4.0	3.9	3.9	3.6	34.1		611	2684	3582	34671
1975	3.2	5.5	4.3	9.7	34.7		53	642	2799	16075
1976	3.4	3.6	3.5	9.0	34.3		371	8607	2158	16988
1977	3.6	3.9	3.6	6.1	34.2		387	6223	2533	17764
1978	3.9	4.0	3.8	6.1	34.4		406	6334	4552	16762
1979	4.1	3.8	3.9	5.8	34.4		588	9080	3317	20073
1980	3.9	3.6	3.7	5.9	34.3		773	14357	1545	15967
1981	3.8	3.6	3.7	5.8	34.3		190	2329	2207	13891
1982	3.9	7.3	5.0	10.8	35.0		702	13242	2004	14684
1983	4.0	4.3	5.7	11.7	35.1		954	17108	2385	19527
1984	4.4	5.3	4.8	12.6	34.6		907	17819	2961	20228
1985	3.5	5.2	4.0	9.0	34.8		671	17842	2872	20277
1986	5.9	3.7	5.2	8.9	34.9		720	17152	3587	28869
1987	9.2	3.7	8.7	13.9	35.3		773	21752	3537	43685
1988	4.4	10.2	7.1	11.7	35.2		708	15549	2092	23146
1989	4.0	6.8	4.9	13.5	35.3		1235	34220	3028	47484
1990	2.8	8.5	6.9	6.2	34.5		4616	64593	6279	66887
1991	3.1	9.1	4.4	6.6	34.7		3359	39434	4727	41406
1992	4.7	3.5	4.9	6.6	34.5		1648	26311	4421	31071
1993	4.4	3.5	3.7	4.4	34.2		724	15636	2827	21564
1994	2.4	3.4	2.5	9.1	34.3		1075	8441	2116	9365
1995	3.3	3.2	3.2	5.6	34.4		285	4432	1843	6158
1996	3.4	3.4	3.3	5.5	34.3		92	66	604	1022
1997	3.4	3.5	3.4	5.4	34.5		14	196	379	424
1998	8.4	3.6	6.4	10.4	35.0		40	433	561	797
1999	4.4	8.6	5.2	7.9	34.3		17	320	359	758
2000	4.1	4.1	4.0	6.3	34.3		46	102	2545	3230
2001	4.0	3.8	3.9	6.0	34.5		0	0	676	3127
2002	6.0	4.2	4.7	5.7	34.5		201	1167	2016	2900
2003	4.8	9.5	4.8	6.7	34.6		8	93	2821	1817
2004	4.0	3.7	3.9	6.6	34.6		15	210	1402	3015

[3]Chapter 4. After You've Gone: Deep-Sea Fishes Found to be Critically Endangered

The World Conservation Union, formerly The International Union for the Conservation of Nature and Natural Resources (referred to as IUCN hereafter), criteria (IUCN 2006) have been used to classify marine fishes as species-at-risk since 1996 when Atlantic cod *Gadus morhua* was listed as vulnerable (Hutchings 2001). Deep-sea fishes have not been evaluated using these criteria, despite their extreme life-history traits and declining trends in biomass and mean size (Haedrich 1995). This omission has likely resulted from lack of knowledge and data for most species. Despite this paucity of information, research survey results indicate that five deep-sea fishes have declined over a seventeen-year period in Canadian waters of the Northwest Atlantic to such an extent that they meet the IUCN criteria for critically endangered. These results suggest immediate action is required for the sustainable management of deep-sea fisheries.

Many of the world's resources are being extracted at unsustainable rates (Pauly et al. 2002). The vastness of the ocean and the view that marine fishes are highly fecund led to the assumption that species could not become extinct in the sea (Pauly et al. 2002). Only recently has attention focused on the decline of marine taxa, such as sharks, tuna, cod, and sea turtles (Graham et al. 2001, Jackson et al. 2001, Pauly et al. 2002, Baum et al. 2003, Myers and Worm 2003).

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[5] Part of this chapter was published as J.A. Devine, K.D. Baker and R.L. Haedrich. 2006. Deep-sea fishes found to be critically endangered. *Nature* 439: 29. Format has been modified from the original publication.

As the shelf fisheries in the Northwest Atlantic began to collapse in the 1960s and 1970s, fisheries shifted to the harvest of deep-sea fish species (Fogarty and Murawski 1998, Moore and Mace 1999, Haedrich et al. 2001). Deep-sea fishes are highly vulnerable to disturbance; they exhibit K-selected life history traits, such as late maturation, extreme longevity, low fecundity, and slow growth, which make recovery subsequent to disturbance difficult (Moore and Mace 1999, Koslow et al. 2000, Clark 2001). The species evaluated in this study can live to 60 years of age, grow to be over one meter in length, and mature in their late teens. Many deep-sea fishes form aggregations on seamounts and flat seafloor bottoms, which increases their susceptibility to over-fishing (Koslow 1997). Species diversity peaks at depths of 1,500 meters and thus, fisheries catch many more species than just the target species (Haedrich 1995). Many deep-sea fisheries are discovered, rapidly over-fished, and crash within ten years of their development (Moore 1999, Koslow and Tuck 2001). Even when not targeted by deep-sea fishing, species taken in by-catch usually die. Limited survey data collected over extended periods of time make it difficult to determine the effects of fishing both on target and by-catch species.

Although declines in fishes are evident, there is debate concerning the idea of marine fishes as species at risk. Some researchers feel that The World Conservation Union (IUCN) criteria (see Methods) grossly overestimate the extinction risk for many marine fish species (e.g. Musick 1999). As an alternative, the American Fisheries Society (AFS) developed criteria that consider productivity index parameters, which include population and individual growth, maturation and fecundity parameters from an unexploited population state. Deep-sea fishes fit into the low to very low productivity categories and

do not reflect many of the usual assumptions regarding marine fishes. Based on the AFS criteria, a 70% to 85% decline would be needed to classify a deep-sea fish as vulnerable and further listing would be subject to scrutiny. Little theoretical support exists for the perceptions upon which these criteria are based, and, furthermore, exemption of marine fish from population-decline criterion would be inconsistent with a precautionary approach (Hutchings 2001). As a result, the IUCN criteria were used in this study (see Methods).

For the analysis, I chose five demersal deep-sea species which range in abundance from highly abundant to rare; roundnose grenadier *Coryphaenoides rupestris*, roughhead grenadier *Macrourus berglax,* blue hake *Antimora rostrata*, largescale tapirfish *Notacanthus chemnitzi*, and spinytail skate *Bathyraja spinicauda.* Two species, *C. rupestris* and *M. berglax,* have been subjected to commercial fisheries and all are taken as by-catch in other fisheries, especially those that target deepwater Greenland halibut *Reinhardtius hippoglossoides* and redfish *Sebastes spp.* None were taken in any substantial number, even as by-catch, before the 1970s (NAFO Statistical Bulletins). I used catch data from standardized research trawl surveys in Canadian waters of the northwest Atlantic Ocean from 1978–1994 to determine declines in relative abundance and individual mean size

4.2. Methods

4.2.1. IUCN Red List criteria

A species is assigned to a threat category depending on the projected decline the species has undergone over the past 10 years or 3 generations, whichever is longer (IUCN

2006). Where the causes of the reduction have ceased, are understood, and are reversible, a species is considered critically endangered if the decline is $\geq$ 90%, endangered if the decline is $\geq$ 70%, and vulnerable if the decline is $\geq$ 50%. If the causes of the reduction have not ceased, are not understood, or are not reversible, a species is considered critically endangered if the decline is $\geq$ 80%, endangered if the decline is $\geq$ 50% and vulnerable if the decline is $\geq$ 30%.

4.2.2. Data selection and analysis

The ECNASAP (East Coast North American Strategic Assessment Project) dataset was the source of records in Canadian waters for years 1978–1994 (Brown et al. 1996, Doubleday and Rivard 1981). This database consists of data (numbers and weights) from random stratified scientific survey tows, where strata boundaries are determined by depth. Prior to 1978, sampling gear varied and surveys were not always based on a random stratified design (Doubleday 1981), therefore, data prior to 1978 were not used in the analysis. Survey data for 1995–2003 were obtained for *Coryphaenoides rupestris* and *Macrourus berglax* from the appropriate Department of Fisheries and Oceans branches. In Newfoundland-Labrador waters in 1995, sampling strategy was changed from an Engels 145 bottom trawl to a Campelen 1800 bottom trawl. Campelen trawls have a smaller mesh size, larger net, and are fished for a shorter duration at a slower speed than the Engels trawl. Species-specific correction factors were estimated by completing gear comparison studies for a few commercially important species. This comparison was not done for any of the species in this study; therefore I estimated species specific conversion factors for data from 1995–2003, which was simply the ratio of mean catches 1993–1994

to mean catches 1996–1997. Because IUCN criteria are applied to trends in abundance over time, I used weighted number per tow as a relative index of population abundance where data were weighted by the areas of the strata (square nautical miles). Only strata that were consistently sampled were included in the analysis. The survey extended into new areas during the time period from 1978–2003, and I therefore restricted the analysis to strata that were well-sampled at all times (Hilborn and Walters 1992). Strata must have been sampled for at least half of the time series and for at least two years during the first and last five years of the time series.

Trends in weighted relative abundance over the time period were estimated using a generalized linear model:

$$N=\beta_0 + \beta_{yr}*yr + \beta_{strat}*strat + \varepsilon,$$

where N = relative abundance of a species weighted by area of the strata, yr = year and $strat$ = stratum; a log link and negative binomial distribution were used (Table 4.1). A log link was used because the mean of N is the log of the linear predictor yr. Declines were estimated from the equation $100(1-\exp^{(\beta yr * t)})$ where β_{yr} is the exponential decline and t is time in years. In order to estimate declines over three generations, t = 3*generation time. Generation time was estimated from the formula *age at maturity* + 1/*mortality*. Age at maturity and mortality rates were taken from the literature for all species except *Notacanthus chemnitzi* and *Bathyraja spinicauda*, which are unknown but were inferred from other deep-sea fishes (Bergstad and Isaksen 1987, Murua 2000, Lorance et al. 2001, Magnússon 2001). *B. spinicauda* parameters were inferred from another large skate species sharing similar habitat preferences and *N. chemnitzi* parameters were taken as an average of other deep-sea fishes.

Trends in individual mean size were estimated from the generalized linear model:

$$Size=\beta_0 + \beta_{yr}*yr + \varepsilon,$$

where *size* = mean size (kg per individual) and *yr* = year; a gamma distribution and log link were used (Table 4.2).

4.3. Results and discussion

All species declined in relative abundance (Figure 4.1); declines over the seventeen-year time period ranged between 87%–98% and declines estimated for the IUCN benchmark of three generations ranged between 99%–100% (Table 4.3). Survey data for the additional period of 1995–2003 were obtained for *C. rupestris* and *M. berglax.* The overall declines in relative abundance for these two species over the 26-year time period were 99.9% and 93.3% respectively; estimated declines over three generations were 100% and 99.7% (Table 4.3). According to the IUCN criteria, these five deep-sea fishes can be considered critically endangered in the western North Atlantic. The declines occurred within a timescale equal to or slightly less than only one generation for each of these species. All species except *N. chemnitzi* also declined 25–57% in mean size over the seventeen-year time period (Table 4.4, Figure 4.2). The survey data are inadequate to assess well the status of other deep-sea fishes, but it is reasonable to assume that many others may also be at risk.

Scientific study often lags behind the development and collapse of deep-sea fisheries (Moore and Mace 1999, Haedrich et al. 2001). More detailed research relating to the effects of fishing and the establishment of deep-sea marine protected areas needs to be

pursued; however, lack of knowledge should not delay appropriate conservation initiatives.

Publication of the material contained in this chapter (i.e., Devine et al. 2006) met with considerable interest from many quarters. Objections to its findings were raised within a few weeks by the Fisheries Council of Canada (Patrick McGuinness, through the International Fisheries Council Association, Isaribi 2006) and shortly thereafter by those responsible for species at risk in the Department of Fisheries and Oceans, Newfoundland Region. The story surrounding those objections is told in Chapter 5. In chapter 6, I explore if using statistical rigor instead of comprehensive inclusion of all data when analyzing trends in two grenadier species is appropriate and if the observed trends are related to environmental factors and/or overexploitation.

Table 4.1. Results of generalized linear models: $N=\beta_0 + \beta_{yr}*yr + \beta_{strat}*strat + \varepsilon$, where N= relative abundance of a species weighted by area, yr = year and $strat$ = stratum with log link and negative binomial distribution, for five deep-sea fish species in Canadian waters of the Northwest Atlantic 1978–1994, and for *C. rupestris*[a] and *M. berglax*[a] for 1978–2003. The log likelihood value was used as a measure of goodness of fit of the model.

Species	β_0	Std. Error: β_0	Year	Std. Error: Year	Strata	Std. Error: Strata	Log Likelihood
A. rostrata	9.93	59.05	-0.154	0.676	0.0028	0.0157	-2.58
N. chemnitzi	12.87	54.29	-0.216	0.648	0.0039	0.0135	-1.63
C. rupestris	16.35	67.77	-0.196	0.773	0.0019	0.0174	-4.03
M. berglax	10.76	19.27	-0.125	0.223	0.0005	0.0051	-16.16
B. spinicauda	6.38	25.34	-0.123	0.300	0.0021	0.0069	-3.17
C. rupestris[a]	17.47	36.21	-0.213	0.392	0.0029	0.0138	-5.16
M. berglax[a]	8.28	9.53	-0.104	0.106	0.0024	0.0041	-22.53

Table 4.2. Results of generalized linear models: $Size=\beta_0 + \beta_{yr}*yr + \varepsilon$, where *size* = mean size (kg per individual) for a species and yr = year with a gamma distribution and log link for five deep-sea fish species in Canadian waters of the Northwest Atlantic 1978–1994. The log likelihood value was used as a measure of goodness of fit of the model.

Species	β_0	Std. Error: β_0	Year	Std. Error: Year	Log Likelihood
Antimora rostrata	2.94	1.66	-0.050	0.019	-41.16
Notacanthus chemnitzi	-0.36	0.38	0.008	0.008	-42.10
Coryphaenoides rupestris	2.82	1.42	-0.047	0.017	-41.03
Macrourus berglax	1.31	0.73	-0.018	0.009	-42.09
Bathyraja spinicauda	3.54	0.73	-0.017	0.008	-42.05

Table 4.3. Estimated exponential decline, 95% confidence interval of the decline, generation time, and decline rate over three generations in weighted relative abundance (number/tow) for five deep-sea fish species in Canadian waters of the Northwest Atlantic 1978–1994, and for *C. rupestris*[a] and *M. berglax*[a] 1978–2003. Relative abundance was weighted by the area of the strata.

Species	Decline (%)	95% CI (%)		Generation time (yr)	Decline 3 generations (%)
A. rostrata	92.7	98.7	82.4	17	100
N. chemnitzi	97.5	99.8	95.0	20	100
C. rupestris	96.4	99.4	88.4	17	100
M. berglax	88.1	94.1	80.4	19	99.9
B. spinicauda	87.6	95.9	84.4	21	100
C. rupestris[a]	99.6	99.9	99.1	17	100
M. berglax[a]	93.3	95.6	86.2	19	99.7

Table 4.4. Estimated exponential declines and 95% confidence intervals of the decline in individual mean size for five deep-sea fish species in Canadian waters of the Northwest Atlantic 1978–1994.

Species	Decline (%)	95% CI (%)	
Antimora rostrata	57.1	77.5	18.5
Notacanthus chemnitzi	No decline	--	--
Coryphaenoides rupestris	54.9	74.0	21.7
Macrourus berglax	26.5	44.7	2.4
Bathyraja spinicauda	25.5	43.8	1.3

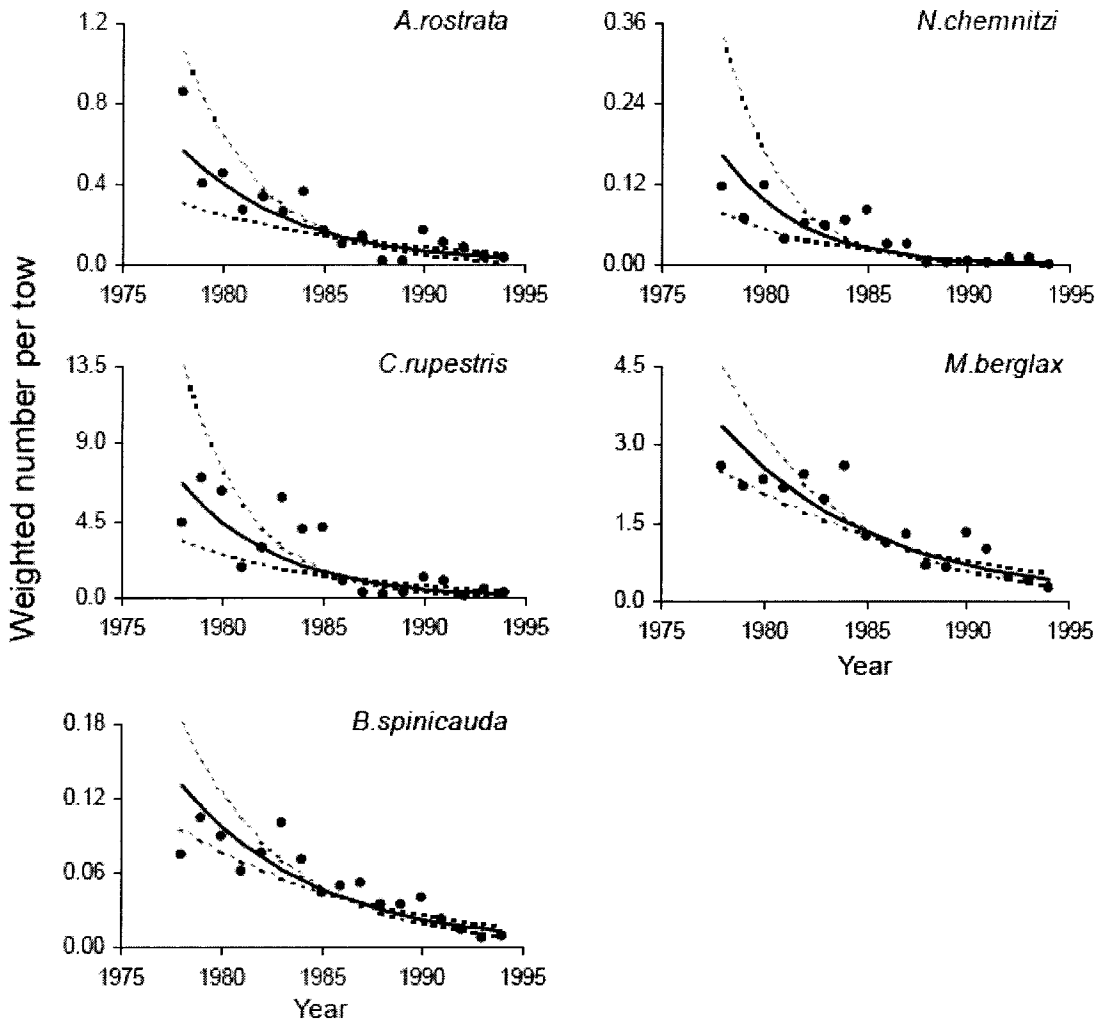

Figure 4.1. Weighted relative abundance (number per tow) over time in research survey data with estimated exponential decline (thick line) and 95% confidence projections of the estimate (dashed lines) for five deep-sea species in Canadian waters of the Northwest Atlantic, 1978–1994.

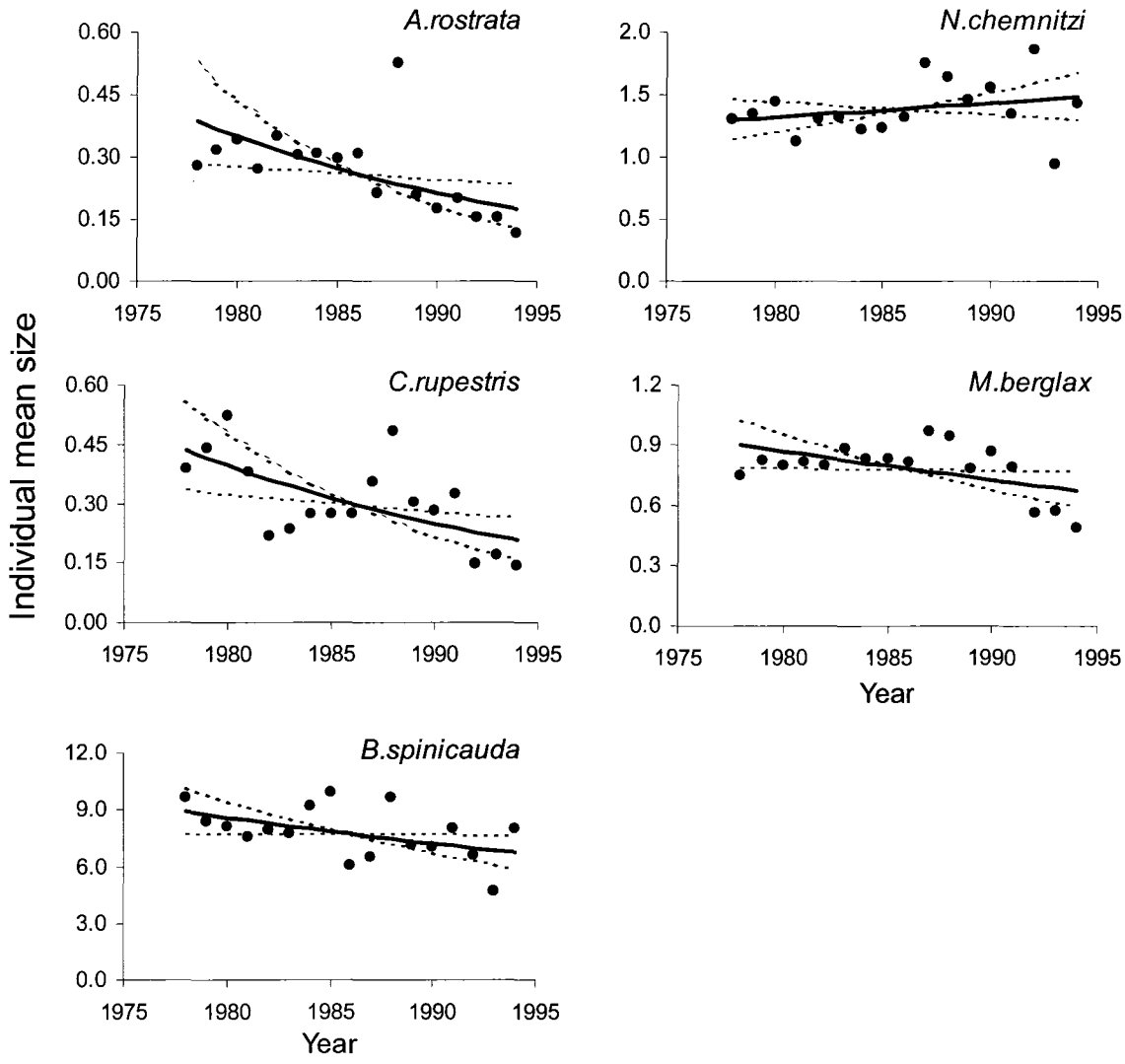

Figure 4.2. Trends in mean size (kg per individual) with 95% confidence projections of the decline (dashed lines) for five deep-sea fish species in Canadian waters of the Northwest Atlantic, 1978–1994.

[4]Chapter 5. These Foolish Things: A Rebuttal to the Nature Paper

After publication of our *Nature* paper (Devine et al. 2006; Chapter 4), we were contacted by Mr. David Kulka, head of Marine Species at Risk, Department of Fisheries and Oceans, informing us of his intention to submit a "Brief Arising" to *Nature* regarding our data analysis. Their main claims were that "a large proportion of the slope species dealt with by Devine et al. occur outside of the surveyed areas both in terms of depth and latitude", and "survey data employed by Devine et al. can in no way be used to distinguish between local affects and actual population decreases or increases". Additional arguments included changes to gear and depth invalidated direct comparisons of the time periods pre- and post-1995, overfishing did not cause the decline of these species, and data after 1994 were not analyzed, although in our possession, because they showed "increasing survey trajectories for at least three of five species after 1994, including *Macrourus berglax*".

We had an initial exchange, in which we offered to jointly analyze data with DFO, but this was rejected. Thus, we felt compelled to construct a more detailed response. Our final response to *Nature*, necessarily limited to approximately 500 words, appears in section 5.2. I also submitted additional material, responding to a few major assumptions and several mistruths regarding our analyses set forth by Kulka et al., included in section 5.3. Thus was in response to 15 additional pages of comments sent to us by Kulka et al. after our initial exchange. In the event that the Brief Arising is ultimately sent to a referee, the referee will see all supplemental material, therefore, we felt obligated to address at least

[4] The responses were written with the assistance of K.D. Baker and R.L. Haedrich.

some of Kulka et al.'s comments. Responses are included in the form submitted and received, including references. All of the material was available to Kulka et al.; their exchanges are omitted here.

5.2. Our Final Response to *Nature*, March 17, 2006

Kulka et al. echo McGuinness[1] in questioning that 5 deep-sea species qualify as critically endangered in Canadian waters[2], but the reports they cite in support of their claim present data on only two. For *Antimora rostrata* the index is an estimate of total biomass and numbers[3] derived from a STRAP program with no accounting for changes in sampling gear, catchability and strata added over time. STRAP analyses provide 95% confidence intervals for each annual estimate, but these are not reported so it is impossible to judge any claim regarding trends. The catch of *Antimora* in commercial fisheries along the shelf edge for 1960-2001 is also presented and has been declining since 1971.

For *Macrourus berglax*, while confidence intervals for biomass estimates are reported[4], the increase in surveys outside Canadian waters is driven by higher values in the last 2 years of the time series (2003 and 2004)[4-6]. But VPA estimates[5] of total adult biomass (IUCN criteria reference adult trends) reveal an 80% decline 1993-2004 (about two-thirds of a *Macrourus* generation) with 95% confidence intervals of 62-89%. We note also that deep populations of slope species are not separate from shallow ones because of ontogenetic migrations. It is to be expected that overall biomass might continue to grow at depth for a considerable period of time after declines in numbers are noted in shallower regions, with a time lag of generations that span decades.

Both analyses derived estimates from all strata sampled regardless of whether sampling was consistent over the years. For *Macrourus*, effort was made to correct for this with the result that the apparent increase diminished. Because deeper strata were added in later years and because bigger fish are found deeper, the effect was to inflate the later estimates, a problem the authors acknowledge[6].

It is incorrect and misleading to characterize our data as representing fringe populations. Slope-dwelling species[7] occupy a rim around the ocean basins; our samples reach 1000 meters for all species and 2200 meters for grenadiers, encompassing much of the slope in our region. The grenadiers are endemic to the North Atlantic, with perhaps 25-30% of their entire distribution in Canadian waters. Regardless, the argument is weak in light of the recognition that trouble at the edge of a range presages trouble over the entire range[8]. Local depletions should be replenished from unfished portions of the population when effort lessens[9], but we see no evidence of that here.

That distribution shifts have occurred is unsupported speculation; the reference cited has nothing to do with distribution. Temperature fluctuations in the area have been very low

and are unlikely to have caused shifts[10], a fact recognized even by those who originally proposed this happened with *Coryphaenoides*[11]. Overfishing is documented as a problem for grenadiers and is especially clear for *Coryphaenoides*[12] in a deep-sea fishery that began in the late 1960s and was exhausted by 1992. In the meantime *Coryphaenoides* populations have declined right across the Atlantic[13] and *Macrourus* landings are in decline off Newfoundland[5-6].

We agree that conservation is important. Canada's Department of Fisheries and Oceans operates explicitly under a precautionary principle wherein "the absence of full scientific certainty shall not be used as a reason for postponing decisions where there is a risk of serious or irreversible harm". The tired argument that "more science is needed" puts Kulka and Simpson clearly at odds with their Department's policy. As for science, our findings were predicted from first principles some time ago[14] and the likelihood remains that any recovery will be in proportion to the extent of the observed declines[15].

[1] http://www.suisankai.or.jp/topics_e/isaribi/isaribi_48.pdf, Japan Fish. Assoc. ISARIBI No. 48. (2006).
[2] Devine, J. A., Baker, K. D. & Haedrich, R. L. *Nature* **439**, 29 (2006).
[3] Kulka, D. W. & Simpson, M. R. CSAS Res. Doc. 03/022 (2003).
[4] Murua, H. & Cárdenas, E. de.. *e-J Northw. Atl. Fis. Sci.* **37** (2006).
[5] Gonzáles and Murua NAFO SCR Doc. 05/54 18p. (2005).
[6] Murua, H., Gonzáles, F, & Power, D. *e-J. Northw. Atl. Fish. Sci.* **37** (2005).
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[8] Fraser, D. *in* Darling, L.M. Proceedings of a conference on the biology and management of species and habitats at risk, Kamloops, B.C. pp. 49-52 (2000).
[9] Maury, O. & Gascuel, D. *Aquat. Living Resour.* **14**, 203-210 (2001).
[10] Atkinson, D.B., Power, D. & Kulka, D.W. NAFO SCR Doc. 93/74 20p. (1993).
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[12] Haedrich, R. L., Merrett, N.R & O'Dea, N. *Fish. Res.* **51**, 113-122 (2001).
[13] Jørgensen O.A. NAFO SCS **31**, 21-56 (1998), Gordon, J.D.M. *Cont. Shelf. Res.* **21**, 987-1003 (2001), *J. Northw. Atl. Fish. Sci.* **31**, 57-83 (2003), Large, P.A. et al. *J. Northw. Atl. Fish. Sci.* **31**, 151-163 (2003), Lorance, P., and Dupouy, H. ICES CM 1998/O:19 (1998), Janusz, J. et al.. Sea Fisheries Institute. Gdynia, Poland (1999).
[14] Koslow, J.A. et al. *ICES J. Mar. Sci.* **57**, 548-557 (2000), Roberts, C.M. *Trends Ecol. & Evol.* **17**, 242-245 (2002).
[15] Hutchings, J.A. *Nature* **406**, 882-885 (2000).

5.3. Supplemental material submitted March 17, 2006

The language and objections in the Matters Arising and Supplemental Material are strikingly similar to a letter that has already been published in a Japanese fisheries trade journal (http://www.suisankai.or.jp/topics_e/isaribi/isaribi_48.pdf). The author of the letter is from the Fisheries Council of Canada, an industry lobby group based in Ottawa.

Kulka et al. insinuate that we have biased our results by selective use of data. We repeat the point made in our main response: we used all the data available to us and had access to no other data. When we first learned of Kulka et al.'s dissent, we offered to try to resolve the issue by analyzing their Campelen series according to the protocol we applied (consistently sampled strata, weighted number/tow, explicit level of uncertainty), and we asked them to share the data with us. They declined giving us access to the data with the excuse Nature does not allow additional analyses. As such, we cannot address any of their comments regarding their analysis of the survey data 1995-2003.

In addressing Kulka et al.'s 15 pages of supplemental material, we selected a few main points with the focus on those not addressed directly in our response to the Matters Arising.

We never stated our conclusions pertained to the entire northwest Atlantic. We specified our analysis was for Canadian waters because of the limited data we had access to and permission to use. The data we used were not *only* (their italics) shallow waters. Our analysis went to 1000 meters for all species and 2200 meters for the two grenadier species, i.e. across most of the slope.

In response to their query:
"We raise the question of what constitutes the "continental slope" of Canadian or northwest Atlantic", we defer to Gordon et al. (1995) who clearly define continental slope waters as depths between 200 and 2000 meters.

Kulka et al.'s "expectation" (their word) that we used only Newfoundland data is incorrect. We used data from the full Canadian survey, which does include deepwater areas beyond Newfoundland. We did not restrict the analysis to only include data from areas where we expect to find the species of interest because 0 catches were deemed important. Filtering the data to exclude where a species is not found (0 catches) also ignores the stratified design of the survey and is statistically incorrect. We assumed differences between ships towing the same gear to be minimal for the analysis, as did Brown et al. (1996). All tows were standardized to a 30-minute tow for the Engels trawl and to a 15-minute tow for the Campelen. We also feel the need to state that most 0 catches were, as Kulka et al. point out, from regions other than Newfoundland and that a 0 is a 0 regardless of the gear or ship used. It is not clear to us whether 0 catches are included in any of the *Antimora* data presented by Kulka and Simpson (2003). This is also the reason why we insist that confidence limits must be explicit; one function they serve is to capture any variability introduced by the factors stated by Kulka et al.

The conclusion Kulka et al. "reasonably" (their word) drew about our data extending only to 700 meters is incorrect; we have addressed this above. Murua and de Cárdenas (2006) found that the slope-dwelling grenadiers including *Macrourus berglax* were replaced at 2000 meters, by another grenadier species characteristic of continental rise and abyssal

depths. Our data did fully sample the range of *Macrourus*. We agree that the data used did not sample the full depth range for *Antimora,* which does range out onto the rise but not abyssal depths.

We reiterate our statement concerning "fringe" populations: the argument is weak in light of the recognition that trouble at the edge of a range presages trouble over the entire range (Fraser 2000). There is no evidence supporting the puzzling claim that these populations are "well separated from the centre of the mass". There is no evidence shown to back up the claim that "density changes at the fringe do not represent population changes". In fact, there is a body of literature that states this to be a common misconception (Lomolino and Channell 1995, 1997, Fraser 2000, Channell and Lomolino 2000).

We have addressed the trends in the papers cited by Kulka et al. as showing increasing biomass in our main response and do not feel we need to go into them again here in any detail.

We did apply a species-specific scaling factor to scale Campelen catch to Engels. Kulka et al. incorrectly state we used the factor estimated by Bundy et al. (2000); we used a similar method but estimated the scaling factor individually for each species.

We have addressed the imagined distribution shifts in our main response. Temperature fluctuations at depths these species are distributed were found to be only a few tenths of a degree and, as stated by Savvatisky (1991), Atkinson et al. (1993), and Atkinson (1995), would not cause a massive distribution shift. This is merely speculation by Kulka et al.

To entertain Kulka et al.'s idea of a distribution shift, we offer our own speculation: suppose the grenadier population shifted southeastward, out of range of the Canadian survey towards the Flemish Pass/Flemish Cap. Aggregation can suggest an increase in biomass that does not reflect the true state of the population and can be highly misleading (Rose and Kulka 1999). Even if *Macrourus* is not targeted, there is an aggressive Greenland halibut fishery operating in the area and *Macrourus* is taken as bycatch (Paz and Casas 1995, Savvatimsky and Gorchinsky 2001). Murua (2001) found that *Macrourus* is fully recruited to the fishery at age 8, whereas the age at 50% maturity is 13-16 years (Murua and Motos 2000, Murua 2001), a situation that inevitably will lead to serious declines.

Generation time estimates for the species are described in the methodology accompanying the original paper. Theoretical but well-founded estimates were used for *Bathyraja spinicauda*, as also explained in the methodology and references cited therein.

Current thinking regarding the status of *Dipturus laevis* was brought to our attention post-publication.

Kulka et al. point out that we chose to cite many of the CSAS and NAFO documents in our response. Most of the information regarding survey design and gear catchability is published in these documents and nowhere else. It does not indicate that "we have confidence in their content" (their words), merely that the information is found nowhere else. The papers of a "generic nature" (their words) and not relating to the species at hand discuss first principles. The burden of proof does not lie in showing that the principles exist, but rather that they do not hold true.

We decline to respond to the remainder of Kulka et al.'s 15-page response to our initial response. We feel we have covered the main points; this discussion could probably continue for another 30 pages, but we simply have no stomach for that. This language is perhaps a bit strong, but even Kulka et al. refer to these as "minor issues".

Gordon, J.D.M., Merrett, N.R., & Haedrich, R.L. *in* Hopper, A.G. Deep-water fisheries of the North Atlantic oceanic slope. Kluwer Academic Publishers, London. (1995)

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Atkinson, D.B. *in* Hopper, A.G. Deep-water fisheries of the North Atlantic oceanic slope. Kluwer Academic Publishers, London (1995), Savvatisky, P. NAFO SCR Doc 91/8 22p. (1991).

Rose, G.A. & Kulka, D.W. *Can. J. Fish. Aquat. Sci.* **56**:118-127 (1999).

Savvatimsky, P.I., & Gorchinsky, K.V. NAFO SCR Doc. 01/9, 12 pp. (2001).

Murua, H. NAFO SCR Doc 01/29, 19 pp (2001).

Murua, H. & Motos, L. *Sarsia* **85**: 393-402 (2000).

5.4. Response from *Nature*, May 3, 2006

Nature declined to publish the Brief Arising, although the original authors have the right to appeal. It was reviewed and while both referees thought there were points that

merited discussion, Kulka et al.'s main claim that the survey was inadequate to assess these deepwater stocks was described as "bogus".

5.5. What next?

The exchange chronicled above did raise a number of additional questions regarding the analysis. In the next chapter, I explore many of the questions raised regarding both data analysis and statistical rigor with a detailed examination of the two North Atlantic endemic species, *Macrourus berglax* and *Coryphaenoides rupestris*.

[5]Chapter 6. How Long Has This Been Going On? Population Trends and Status of Two Northwest Atlantic Grenadiers

Continental slopes, those regions of the ocean bottom between depths of 200 and 2000 meters, make up only 8.8% of the ocean area, but are complex and dynamic environments with features such as submarine canyons, irregular bathymetry, outcrops, mudslides and internal waves (Gordon et al. 1995, Haedrich et al. 2001). Food availability is restricted; except for vent and seep environments, all deep-water production relies on photosynthesis in surface layers (Gordon et al. 1995, Haedrich 1996). This dependence on production at the top of the water column results in life-history characteristics for many slope-dwelling fish species that include slow growth, late maturation, low fecundity and extreme longevity (Koslow 1996). Deep-sea fish communities are diverse and widespread, zoned by depth, and, in most situations, no one single species dominates (Haedrich and Merrett 1992, Gordon et al. 1995). All these factors combine to make it clear that efforts to expand deep-sea fisheries will experience considerable difficulties in terms of sustainability and impacts on many non-target species (Koslow et al. 2000, Boyer 2001, Roberts 2002).

The broad geographic ranges of many deep-sea fishes, some on the scale of ocean basins, create assessment and management difficulties because species are distributed across management region boundaries and often extend into international waters.

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[5] Part of the chapter is in review as Devine, J.A. and Haedrich, R.L. Population trends and status of two exploited Northwest Atlantic grenadiers, *Coryphaenoides rupestris* and *Macrourus berglax*. *In* Orlov, A. and Iwamoto, T. Grenadiers of the World Oceans: Biology, Stock Assessment and Fisheries. AFS Symposium Series.

The unregulated exploitation of most deep-sea fisheries further complicates the problem. Fisheries on species with K-selected life history strategies – those species that inhabit relatively stable environments, attain large size, defer reproduction in favour of growth and produce smaller numbers of more developed offspring – show signs of overexploitation at lower fishing mortality rates than species with r-selected strategies, and are much slower to recover from exploitation (Clark 1995, Koslow et al. 1997). Deep-sea species exhibit a range of life history characteristics ranging from extremely slow population growth to rates not much different from shelf dwelling species (Clarke et al. 2003). Some deep-sea fishes, therefore, may be able to withstand some levels of exploitation while others could be driven to extinction. It is to be expected that the long-lived, late-maturing, low fecundity elasmobranchs would fall in the latter category. Indeed, the once-common shallow water winter skate *Leucoraja ocellata* is now considered endangered (COSEWIC 2005, IUCN 2006), and several species of pelagic sharks in the northwest Atlantic and Gulf of Mexico have declined rapidly (Baum et al. 2003, Baum and Myers 2004).

Grenadiers are common slope species in the North Atlantic. Two of the most well known are roundnose grenadier *Coryphaenoides rupestris* and roughhead grenadier *Macrourus berglax*, which are endemic in temperate to Arctic continental shelf and slope waters around the North Atlantic rim (Leim and Scott 1966, Savvatimsky 1969, Marshall and Iwamoto 1973, Geistdoerfer 1986, Haedrich and Merrett 1988, Scott and Scott 1988, Cohen et al. 1990, Atkinson 1995, Kelly et al. 1997, Haedrich et al. 2001). *M. berglax* is the only representative of its genus in the northern hemisphere. Roughhead grenadier inhabit temperatures ranging from approximately -0.5 to 5.4 °C (Atkinson and Power

1987) and depths of 400 to 1200 meters (Parsons 1976, de Cárdenas et al. 1996) although they have been found to 2700 meters (Wheeler 1969). Roundnose grenadier are commonly found at temperatures of 3.5°–4.5°C (Scott and Scott 1988) and depths of 600–800 meters (Haedrich et al. 2001), but range to 2500 (Atkinson 1995) and have even been reported to 3000 meters (Sahrhage 1986). Both species are long-lived, late-maturing, slow-growing, have low fecundity (Scott and Scott 1988, Cohen et al. 1990, Zaferman 1993, Kelly et al. 1997) and are therefore vulnerable to over-fishing.

Commercial fisheries have exploited both species. The commercial fishery on *Coryphaenoides rupestris* in the Northwest Atlantic began in the mid-1960s, peaked in 1971 at approximately 80,000 tons and quickly declined (Haedrich et al. 2001). Quotas appear to have been set without taking into consideration the biology of the species (Atkinson 1995); most basic biological information was not gathered until 15–25 years after the fishery began (Haedrich et al. 2001). No directed fishery for *C. rupestris* has existed in NAFO Subareas 0 and 1 (northern Labrador Sea) since 1978 (NAFO 2005) and a moratorium has been in place since 1996 in Canadian waters of Subareas 2 and 3 (Power 1999, Figure 6.1). *Macrourus berglax* is becoming an increasingly important commercial species in the Northwest Atlantic; however, the fishery is unregulated and *M. berglax* is mainly taken as by-catch in the Greenland halibut *Reinhardtius hippoglossoides* fishery (Costas and Murua 2005). Recently, González and Murua (2005) noted the importance of collecting information on the "new" resource *Macrourus*, especially in light of the collapse of traditional groundfish resources. Both roundnose and roughhead grenadier in the northwest Atlantic are recruited to the fishery before they fully mature (Atkinson 1995, Murua 2003).

Given the life-history characteristics of these species, one would expect they might be in trouble and indeed that is the case. Devine et al. (2006) evaluated population trends in several deep-sea fish species and determined that five meet the World Conservation Union (IUCN) criteria for critically endangered; among those are *Coryphaenoides rupestris* and *Macrourus berglax.*

Estimating abundance and population trends in deep-sea species can pose difficulties both in terms of sampling and analysis (Priede and Merrett 1996). Acoustic survey methods are often not appropriate for sampling many deep-sea species because of species identification problems and physiological adaptations, including loss of the swimbladder that reduces their effectiveness as sound reflectors (Clark 1996). Trawl surveys remain one of the best methods to monitor deep-water species and are the standard reference for fisheries worldwide (Sissenwine et al. 1983).

Much debate exists over pinpointing the cause of changes in fish populations. There have been many well-documented dramatic shifts in abundance thought to be primarily caused by changing environmental conditions (e.g., Beamish et al. 1999, Klyashtorin 1998, Bakun and Broad 2003, Hjermann et al. 2004). Overexploitation has also been blamed for causing fish populations to collapse (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1997, Bianchi et al. 2001 Myers and Worm 2003). Most likely, as a few studies have advocated, changes are due to a combination of factors that act in concert but at different spatial and temporal scales (Radovich 1982, Zwanenburg 2000, Shelton et al. 2006, Devine et al. 2007).

In analyzing large sets of fisheries time series survey data, a compromise has to be struck between comprehensive inclusion of all data and statistical rigor. Emphasis on

rigor requires that only data meeting very specific criteria are admitted to the analysis, with the result that breadth of coverage may be lost. This loss can be particularly problematic for deep-sea fish species where ranges are known to be wide but sampling effort and comprehensive cover vary over time. Recognizing this dilemma, I assessed several approaches to analyzing population changes in *Coryphaenoides rupestris* and *Macrourus berglax* that explicitly deal with differing degrees of data filtering and the comprehensiveness of associated metrics. I then examined how trends determined for populations in the Northwest Atlantic are related to environmental factors and/or overexploitation. I focused particularly on the potential effects of ocean climate and targeted fisheries. Finally, I discussed the life history and ecological characteristics of these two species that may have led to the dramatic declines noted in Devine et al. (2006).

6.2. Sources of data

6.2.1. Response variables

The ECNASAP (East Coast North American Strategic Assessment Project) dataset was used as the source of grenadier records in Canadian waters for years 1978–1994 (Doubleday and Rivard 1981, Brown et al. 1996). Survey data for 1995–2003 were obtained from the appropriate Department of Fisheries and Oceans (DFO) branches. These data were collected in stratified random scientific surveys, where strata were determined by depth. Data prior to 1978 were not used in the analysis because surveys were not always based on a stratified random design (Bishop 1994). Data after 1995 posed some problems because of spatial modifications in the survey design and a change from an Engels 145 High Lift otter trawl to a Campelen 1800 shrimp trawl in

Newfoundland-Labrador waters mid-way through 1995. The Campelen trawl has a smaller mesh size, larger net and is fished for a shorter duration (15 minutes versus 30) at a slower speed than the Engels trawl.

Species-specific correction factors were estimated from comparative fishing trials for a few important NAFO species to ensure continuity of the time series after the gear change (Warren 1997), but that analysis was not done for the two grenadier species. Therefore, I converted Campelen catches into equivalent Engels catches for data available from 1995–2003 by applying a species-specific conversion factor: the ratio of mean catch 1993–1994 to mean catch 1996–1997 from consistently sampled strata. Limiting the ratio to consistently sampled strata assumed there were little or no changes in abundance or distribution of the two species 1993–1997. Change in abundance may be more difficult to detect because of the gear change. Zero values were not eliminated from relative abundance estimates because catches of zero were deemed to be informative with respect to the status of populations.

6.2.2. Explanatory variables

Six potential explanatory factors were used, including four environmental variables and two variables related to exploitation. Mean sea surface temperatures (SST) from NAFO Divisions 2GHJ3KL, 1960–2004, and for depths of 0–100 meters, were used with Cold Intermediate Layer (CIL) waters, defined as waters deeper than 30 meters and less than 0° Celsius (Drinkwater 1996), excluded. Sea surface temperatures from NAFO Divisions 3MNO were excluded because of their potential to introduce irrelevant anomalies resulting from Gulf Stream influences on the Tail of the Bank and around the

Flemish Cap (Drinkwater 1996). Mean bottom temperatures (BT), 1960–2004, were estimated from NAFO Divisions 2GHJ3KLMNO for depths of 500–2000 meters, which were chosen to include only those depths within the range of the survey. Mean salinity (SAL), 1960–2004, was estimated from NAFO Divisions 2GHJ3KL, from 0–300 meters depth based on Dickson et al. (1988), who found that the effect of Great Salinity Anomalies (GSAs) on Newfoundland-Labrador shelf and eastern Grand Banks extended to 300 meters. Salinity and temperatures data were estimated for 2004 to match the adult grenadier data, which extended to 2004; data were averaged from 2000–2003 because there was little variation in the data over that period. The North Atlantic Oscillation (NAO) Hurrell winter index (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) is one measure of the strength of large-scale atmospheric circulation; a high positive index indicates stronger westerly winds across the North Atlantic and northwesterly winds in the Labrador Sea (Hurrell et al. 2003). Fishing pressure for 1960–2004 was measured as combined landings of *Coryphaenoides rupestris* and *Macrourus berglax* from all fisheries (Catch) and as landings of Greenland halibut from NAFO records (GHCt). Greenland halibut fishing effort could not be used as a measure of exploitation because it was not reported in the early years of the fishery or, if reported, was combined with effort data for other flounder species that could not be separated from Greenland halibut with confidence (ICNAF statistical bulletins). Raw data are in Appendix A.

6.3. Metrics to Estimate Abundance

I used parallel analyses of four different subsets of the data to determine if using all available data provided a better indication of trends than applying increasing degrees of

statistical rigor. The abundance index was stratified number of fish per tow. In these analyses of different subsets of data I used:

(1) all data from Canadian waters;

(2) only fall data in all Canadian waters because seasonal differences may affect catches. Spring data were not included because those surveys tended to sample shallower waters where grenadiers are usually not found. Costas and Murua (2005) reported that only autumn surveys adequately sampled the distributional range of the grenadiers.

(3) data from only those strata that were sampled consistently (as recommended by Hilborn and Walters 1992). Spatial modifications were made to the survey area over the time period studied; offshore strata were added in the 1990s and in 1995, extending coverage deeper than 1500 meters (Brodie 2005). To address these changes to the survey design, I included only strata that were sampled for at least half of the time series and for at least two years during the first and last five years of the time series. Although this strategy addressed spatial changes to the survey area, it eliminated most of the survey data from recently added deep-water strata where grenadiers are found. An assumption of this method is that grenadiers did not change their distribution over the time period.

(4) fall data, but only those from consistently sampled strata, as described above; and

I also used number per tow of adults-only for fall surveys from 1977–2004; threat criteria are typically assigned based on trends in adults (IUCN 2006). Because adults were not measured from every tow, there were insufficient data to filter for consistently sampled

strata or for generating a weighted relative abundance index. Raw data are in Appendix A.

6.4 Models

6.4.1. Generalized linear models

All trends in weighted relative abundance over the time period were estimated with a generalized linear model using a negative binomial distribution and log link:

$$N=\beta_0 + \beta_{yr}*yr + \beta_{strat}*strat + \varepsilon,$$

where N = relative abundance (number per tow) weighted by area of the strata, yr = year and $strat$ = stratum. Declines were estimated from the equation $100*(1-\exp^{(\beta_{yr}*t)})$ where β_{yr} is the exponential decline and t is time in years. For adult number per tow, the model was weighted by the number of tows in each stratum because tows differed between strata and years. Residuals were checked to ensure an appropriate model was used.

6.4.2. Time series analysis

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) are two methods of time series analysis only recently applied to fisheries data (e.g., Zuur et al. 2003a,b, Zuur and Pierce 2004, Erzini 2005, Erzini et al. 2005). MAFA and DFA require no pre-selection or de-trending of the data, and allow for an objective exploration of underlying trends in multiple datasets and the external factors that might explain observed trends. MAFA and DFA are multivariate methods designed specifically for shorter time series (at least 15–25 years) and are not burdened by many of the shortcomings of traditional time series analysis. They do not, for example, require long,

stationary and complete time series and are relatively efficient at handling common trends (Solow 1994, Zuur et al. 2003a).

MAFA, a type of principal component analysis (PCA), can be used to extract trends, estimate index functions and for smoothing (Switzer and Green 1984, Shapiro and Switzer 1989, Solow 1994). Whereas PCA will estimate axes (or components) that have a decreasing variance, MAFA estimates axes that have decreasing autocorrelation with time lag 1. Since slowly declining auto-correlation functions indicate the presence of a trend, the first MAFA axis is the main trend underlying the entire time series and other axes represent less important trends. Randomization is used to obtain p-values to determine how many axes to use (Solow 1994). Factor loadings are used to determine the relationship of the response variables to a particular MAFA trend (Zuur et al. 2007). Canonical correlations, or cross-correlations between MAFA axes and response time series, can be estimated for the same purpose. Cross-correlations can be used to determine if significant relationships exist between MAFA trends and explanatory variables.

DFA is a dimension reduction technique that models short, multivariate time series in terms of common trends and explanatory variables (Zuur et al. 2003a,b, Zuur and Pierce 2004). DFA can be used to assess common patterns in time series, evaluate interactions between response variables and determine the effects of explanatory variables (Zuur et al. 2003a). DFA models N time series in terms of M common trends, where M is less than N. DFA is similar to other dimension reduction techniques in that the axes are restricted to smoothing functions over time, but differs in that it assumes trends correlate over time (Zuur et al. 2003a). With DFA the effects of time lags on the explanatory variables can be explicitly evaluated. The number of common trends modelled should ideally be less than

the number of time series used and preferably as small as possible without sacrificing goodness of fit. The larger the number of common trends used, the better the model fit but the greater the number of parameters that must be estimated. Akaike's Information Criterion (AIC) was used initially to determine the optimal model in terms of goodness of fit and the number of parameters; the lowest value of AIC indicates the better model and reflects the tradeoff between the fit of the model (log likelihood function) and the model's complexity (number of parameters) (Sakamoto et al. 1986). Factor loadings and canonical correlations were used to determine the importance of a trend to response variables.

Min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) were fully described in Chapter 2, and an illustration of their use was provided in Chapter 3; I therefore omit a detailed description of their methodology here. Before analysis, all response time series were log10 transformed and both response and explanatory variables were standardized to a mean of zero and a standard deviation of one (Figures 6.2, 6.3). Time lags up to eighteen years for all external factors were included in both MAFA and DFA. The number of lags was chosen based on the length of the environmental data and the generation time for both grenadier species; generation time for *C. rupestris* and *M. berglax* is 17 and 19 years respectively (Murua 2000, Lorance et al. 2001).

6.5. Results

6.5.1. Generalized linear models

Increasing statistical rigor to improve consistency resulted in tighter confidence intervals around the estimated decline (Table 6.1). Including all available data resulted in wide confidence intervals, especially for *Macrourus berglax*, where the 95% confidence

interval of the estimated decline encompassed zero. Including only fall survey data from all Canadian waters eliminated 50% of the data and the 95% confidence interval for *M. berglax* still encompassed zero. Limiting the data to consistently sampled strata eliminated 38% of all data, but confidence intervals of the estimated declines for both species were tighter and did not include zero for *M. berglax*. Eliminating strata not consistently sampled resulted in only two tows in depths greater than 1000 meters out of 672 and eliminated all data from NAFO Subareas 0, 1 and NAFO Divisions 2GH, 3M, 4RSTW. Inclusion of only fall data from consistently sampled strata resulted in still tighter confidence intervals, but by that time 75% of the data had been eliminated and decline rates were not noticeably different from consistently sampled strata from all seasons. Estimated decline rates for adult *M. berglax* and *Coryphaenoides rupestris* were 55.7% and 99.7% respectively, and 95% confidence intervals were fairly tight. However, the amount of data used to generate estimates for adults was much less than those using the survey indices (juveniles and adults) because grenadiers were not measured from all tows and zeros were not recorded in the data unless there were no adults in a particular tow. Residuals were checked to ensure appropriate model was used; residuals were normally distributed, non-homogeneous, and indepent.

6.5.2. Time series analysis

6.5.2.1. MAFA analyses

Three analyses using abundance estimates for both species were performed, either for all data, consistently sampled strata, or adults-only. MAFA identified one main, significant trend in relative abundance of the two species using all data (autocorrelation =

0.691, $p<0.001$, $n = 2$) or adult indices (autocorrelation = 0.896, $p<0.001$, $n = 2$); two significant trends were identified using consistently sampled strata (trend 1: autocorrelation = 0.855, $p<0.001$, $n = 2$; trend 2: autocorrelation = 0.26, $p=0.04$, $n = 2$). Using all data, abundances for both species declined until 1995, and then increased (Figure 6.4). Abundances of both *Coryphaenoides rupestris* and *Macrourus berglax* were significantly and positively correlated with the trend (correlation = 0.73 (*Coryphaenoides*), 0.99 (*Macrourus*); significance level for correlations = 0.39). The main trend when using only consistently sampled strata was similar, but the increase after 1995 was not as great (Figure 6.4). Abundances of both *C. rupestris* and *M. berglax* were again significantly and positively correlated with the trend (correlation = 0.89 (*Coryphaenoides*), 0.99 (*Macrourus*); significance level for correlations = 0.39). Although the analysis indicated a second significant trend, the autocorrelation was low. MAF2 varied considerably; however, a wobbly oscillation appeared to underlie the variation (Figure 6.4). Both of these factors indicated that MAF2 is a collection of the noise components in the series (see Chapter 2). The main trend in adults was a decline over time (Figure 6.4). Both *C. rupestris* and *M. berglax* were significantly and positively correlated with the trend (correlation = 0.99 (*Coryphaenoides*), 0.82 (*Macrourus*); significance level for correlations = 0.38). The trends for all data sets increased in abundance from 1995–1996, the year the sampling gear was changed and deepwater strata were added.

All six external factors were significantly correlated with the main MAFA trend for all indices, which was a decline over time. Only the most significant results for each of the data subsets are presented here (Table 6.2). Five out of the six factors were significantly

related to the second trend for consistently sampled data; only grenadier catch was not related to this trend. Both measures of exploitation (grenadier and Greenland halibut landings) had the greatest number of significant correlations with the MAFA trend for all indices. Salinity and bottom temperature tended to be significantly correlated with the trend at short lags, whereas the NAO winter index was significantly correlated at long lags.

Out of 114 combinations of explanatory variables and lags used for analyses of all data and for consistently sampled strata, 23 were significantly correlated to the MAFA trend for all survey data and 42 were significantly related to the trend in data from consistently sampled strata. Out of 108 combinations of explanatory variables and lags used for adults, 55 were significantly correlated with the MAFA trend. By chance alone, six correlations per data subset (twelve correlations for consistently sampled strata) would be expected to be significant at the 5% level. That so many variables were significantly related to the trends indicates that strong relationships exist between the explanatory variables and the trends.

6.5.2.2. DFA analysis

DFA models with lagged explanatory variables gave a better fit than did models with no lags, and two-explanatory variable models gave a better fit than one-explanatory variable models. The best results, or those models with the lowest AIC value, for all datasets were from diagonal covariance matrix models. Plots of observed and fitted abundance for the best DFA model for each species are given in Appendix B.

6.5.2.2.1. All data

The diagonal elements of the error covariance matrix for the one-trend model (**I**, one-trend model = 0.02, 0.15) in relative abundance using all survey data were higher than for the two-trend model (**I**, two-trend model = 0.01, 0.09), indicating that there was still residual information not explained by the one-trend model. The best model using all data was a two-trend, two-explanatory variable model with grenadier catch lagged 15 years and Greenland halibut catch lagged 1 year (1 common trend, AIC = 105.5; 2 common trends, AIC = 102.1, Table 6.3). The main trend in relative abundance was a gentle decline 1978–1995, an increase until 1997, and then a steeper decline to 2003 (Figure 6.4a). The second trend remained fairly stable until 1995, and then decreased abruptly (Figure 6.4b). Factor loadings indicated both species were highly and positively correlated with the main trend (0.52 *Macrourus;* 0.65 *Coryphaenoides*), whereas both were negatively related with the second trend (-0.38, *Macrourus*; -0.31 *Coryphaenoides*). A decline in the trend is related to a decline in abundance if the factor loading or canonical correlations are positive. A negative relationship indicates the trend for the species is the opposite of what is shown. *Macrourus* and *Coryphaenoides* relative abundance was apparently increasing after 1995, the year of the gear change and addition of deep-water strata. Estimated regression parameters for individual species show *Coryphaenoides* had a strong relationship with grenadier catch lagged 15 years whereas *Macrourus* had a strong relationship with Greenland halibut catch lagged 1 year (Table 6.4). The cross correlation between Greenland halibut catch at lag 1 and grenadier catch

at lag 15 was significant (correlation = -0.47, correlations $\geq$ 0.40 were significant at the 5% level), as would be expected.

6.5.2.2.2. Consistently sampled strata

A one-trend, two-explanatory model (Greenland halibut catch lagged 1 year and NAO winter index lagged 14 years) was the best model for consistently sampled strata (AIC = 75.6, Table 6.3). This finding contradicts the MAFA findings, where two trends were identified as being significant. Inspection of the diagonal elements of the error covariance models indicated little residual information was unexplained by the one-trend DFA model ($\mathbf{I} \leq 0.14$). The trend was a decline over time (Figure 6.5). Factor loadings and canonical correlations show that both species are highly and positively related to the trend (Table 6.5). Regression parameters indicated that *Coryphaenoides* was strongly related to Greenland halibut catch lagged 1 year and *Macrourus* was strongly related to NAO winter index lagged 14 years (Table 6.4). The cross-correlation between Greenland halibut catch at lag 1 and NAO index at lag 14 was not significant (correlation = -0.09, correlations $\geq$ 0.40 were significant at the 5% level).

6.5.2.2.3. Adults-only

The "best" DFA model when analyzing relative abundance of adults from autumn research surveys was a one-trend, two-explanatory variable model, with Greenland halibut catch lagged 8 years and salinity lagged 12 years (AIC = 85.9, Table 6.3, Figure 6.6). The diagonal elements from the error covariance matrix were low ($\mathbf{I} \leq 0.23$) indicating there was little residual information remaining. Addition of a second trend showed a straight line and therefore no further trend in the data. The trend showed a

decline until 1995, after which the trend remained fairly stable although at a low level. Abundance of both species were highly and positively correlated with this trend (Table 6.5). *Coryphaenoides* was strongly related to Greenland halibut catch lagged 8 years and *Macrourus* was strongly related to salinity lagged 12 years, as indicated by the regression parameters (Table 6.4). Cross-correlation between Greenland halibut catch at lag 8 and salinity at lag 12 was not significant (correlation = -0.03, correlations $\geq$ 0.40 were significant at the 5% level).

6.6. Discussion

The balance between comprehensive inclusion of all data and statistical rigor is not merely a theoretical consideration, but rather one that must be routinely addressed at some stage in any analytical process. A judgement must be made as to when to accept the loss of some information in order to assess, with confidence, the underlying trend in the data. All generalized linear models showed *Macrourus berglax* and *Coryphaenoides rupestris* had declined in abundance, regardless of the index used. The use of some subsets resulted in a substantial loss of data while not vastly improving the models (all data - fall only and consistently sampled strata - fall only), therefore, these data subsets were deemed uninformative. Using all the data (i.e. the most comprehensive approach) showed both species declined in relative abundance, but little confidence could be placed in the trend for *Macrourus* because the confidence intervals included zero. The use of statistical rigor was necessary, not to show that a trend existed, but to have confidence that the trend was real. This is the same technique employed by Devine et al. (2006), where rigor at the expense of comprehensive inclusion was employed to ensure

confidence in the estimated declines of five deep-sea species. When assessing temporal trends under any conditions, ensuring the comparability of the index over time is extremely important. There are two ways to accomplish this objective when surveys are extended into a new area: restrict the analysis to consistently sampled strata, as done here, or correct older estimates by including estimates from the new area (Hilborn and Walters 1992). Amending estimates based on 'what could have been there' involves many assumptions regarding the past abundance of harvested "non-traditional" commercial species, including their distribution.

There is disagreement over whether the Canadian survey truly captures the population trends of *Macrourus* and *Coryphaenoides* and it has been suggested informally that these surveys sample only the fringes of the populations. I investigated this concern by examining other survey data in the Northwest Atlantic that were available in technical documents for the two species: the EU (Spain and Portugal) summer surveys in NAFO Division 3M completed since 1988 at depths to 730 meters (Saborido-Rey and Vázquez 2003, Costas and Murua 2005), the Spanish 3NO survey completed since 1995 and extending to 1500m (Gonzalez-Troncoso and Casas 2005, Costas and Murua 2005), and surveys in Subarea 1 extending to 1500m and completed 1987–1997 and 1995–2004 (Jørgensen 1998, Jørgensen 2004). The surveys were conducted over a shorter time period than the Canadian data that form the basis of most of my analyses, they report catches in terms of biomass and numbers, and they encompass waters beyond Canada's Economic Exclusion Zone; here I focus only on numbers. *Macrourus berglax* abundance increased slightly in the 3M, 3NO and Subarea 1 data. The increase in 3M abundance data is driven largely by the last two years of data and is not significant (linear regression,

log transformed data, $F_{(1,15)}$=1.96, p=0.18). The increase from deeper surveys in 3NO was borderline significant (linear regression, log transformed data, $F_{(1,6)}$=5.33, p=0.06). Surveys completed off West Greenland (NAFO Subarea 1) show *Macrourus* abundance in Subarea 1 increased, although not significantly (linear regression, log transformed data, $F_{(1,5)}$=5.33, p=0.07). *Coryphaenoides rupestris* abundance in Subarea 1 declined by 76% 1987–1995 and 85% 1997–2004, but declines were not significant (linear regression, log transformed data: $F_{(1,8)}$=1.28, p=0.29; $F_{(1,5)}$=3.89, p=0.11). The data from surveys outside Canadian waters adds information to the general picture regarding population trends, but the results are rather inconclusive. It is difficult to determine, with much confidence, the true trend because any increase or decrease is not significantly different from zero. The results of various indices could support the argument that the species abundance appear to be relatively stable in recent years. However, Costas and Murua (2005) use various survey data (3M, 3NO and Canadian) to present VPA estimates of *Macrourus* spawner biomass; these reveal a significant 80% decline 1993–2004 (about two-thirds of a *Macrourus* generation) with 95% confidence intervals of 62–89% ($F_{(1,10)}$=32.7, p=0.0002).

That the Canadian survey data are claimed (*in litt.*) to sample only the edge of the population is an unwarranted and troubling assertion. *Coryphaenoides rupestris* and *Macrourus berglax* are endemic to the North Atlantic and are known to inhabit continental slopes, defined as waters at depths between 200 and 2000 meters (Gordon et al. 1995), which are depths sampled by the Canadian research survey. Regardless, conservation ecology has shown that trouble at the edge of a range presages trouble over the entire range (Lomolino and Channell 1995, 1997, Fraser 2000, Channell and

Lomolino 2000). Additionally, deep populations of slope species are not separate from shallow ones because of ontogenetic migrations. Immature *Coryphaenoides* are found in large groups off Newfoundland, Labrador, Baffin Island and Greenland (Dushchenko and Savvatimskiy 1987). *Coryphaenoides* moves up and down the slope seasonally, migrating to shallower water at the end of summer and shifting deeper in winter (Savvatimsky 1969, Dushchenko and Savvatimskiy 1987, Paz and Iglesias 1994, Atkinson 1995, Jørgensen 1998). *Macrourus* have also been shown to migrate seasonally (Paz and Iglesias 1994) and to follow the 'bigger–deeper' rule in the northwest Atlantic (Savvatimsky 1992, Savvatimsky and Gorchinsky 2001, Murua 2003).

MAFA and DFA found similar trends in relative abundance of *Macrourus berglax* and *Coryphaenoides rupestris*. When using all available data, both types of analysis showed relative abundance increased after 1995, which reflects modifications to the survey design and the gear change. Using data from consistently sampled strata also showed a slight increase after 1995; this trend was not captured in the adults-only data. Consistently sampled strata and adults-only used data sampled from the same strata, indicating that the increase most likely was due to increased catchability of juveniles by the Campelen. The Campelen trawl has been shown to be more efficient at capturing small fish (Warren 1996). The considerable increase in relative abundance shown using all available data must also reflect increased catchability of juveniles, in addition to demonstrating what was known already, i.e. grenadiers are present in the added strata. Application of a conversion ratio, while compensating partially for differences in catchability between the Engels and Campelen trawls, could not compensate for increased catch of small fish, and a length-based index would have been more appropriate. Such an index would require

data from comparative fishing trials, which were unavailable for these two species. Immigration of fish from elsewhere could explain the slight increase seen after 1995 when using data from consistently sampled strata. However, if this was the cause, it should have been reflected in the adult data; it was not. Temperature fluctuations, often stated as the cause of distribution shifts for fish species in general (de Young and Rose 1993, Gomes et al. 1995, Drinkwater 2002 and references therein), are minimal in the deep-sea, to the extent that they are unlikely to have caused shifts (Atkinson 1993). This fact is recognized even by those who originally proposed this explanation for changes in *Coryphaenoides* (Savvatimsky 1991, Atkinson 1995).

MAFA and DFA have shown that many external factors were related to the trends in relative abundance of *M. berglax* and *C. rupestris*. MAFA found the highest correlations were with Greenland halibut, grenadier catch and the NAO index operating on various temporal scales. Dynamic factor analysis found Greenland halibut catch was an important variable for all trends in relative abundance at different lags; grenadier catch and environmental factors were also related to different indices.

That measures of exploitation were found to be important for understanding trends in grenadier relative abundance is not surprising. In the North Atlantic, combined grenadier catch over the entire period of fishing, 1965–2004, was just over 1,000,000 tonnes (mt) (FAO data). The boom-and-bust story of the *C. rupestris* fishery is well known (Haedrich et al. 2001). As the fishery collapsed in the northwest Atlantic, catches increased in the northeast (Figure 6.7). In the Northwest Atlantic, a moratorium has provided *C. rupestris* some protection since 1978 in Subareas 0 and 1 (NAFO 2005) and since 1996 in Canadian waters of NAFO Subareas 2 and 3 (Power 1999), but *Macrourus berglax* is

becoming an increasingly important commercial species. Currently, *Macrourus* catch is unregulated and the species is mainly taken, often in high numbers, as by-catch in the Greenland halibut fishery operating in NAFO Divisions 3LMNO (Costas and Murua 2005). In the Russian trawl fishery for Greenland halibut, by-catch of *Macrourus* has been as much as 2–3 tons per haul (Savvatimsky and Gorchinsky 2001). In addition to the sometimes high by-catch rate, a high degree of misreporting of the by-catch exists for the Russian longline fishery (Savvatimsky and Gorchinsky 2001). *Macrourus* officially reported by-catch is 5% of the catch in the Russian fishery, but true levels may actually be as high as 9–13% at depths of 800–1200 meters, and 24–25% at depths 1200–1400 meters (Savvatimsky and Gorchinsky 2001). In addition to being taken as by-catch in the Greenland halibut fishery, *M. berglax* is also captured in small amounts in the Flemish Cap shrimp fishery (Bakanev 2002, 2003). *Coryphaenoides* was captured in high amounts in the Greenland halibut fishery in the Flemish Pass when the fishery began in the 1990s; catches were considered some of the highest by-catch rates for any species in that fishery (Gorchinksy and Savvatimsky 1994). Durán et al. (1997) found *Coryphaenoides* and *Macrourus* were two of the seven most commonly caught deepwater species in the Spanish deepwater Greenland halibut fishery in NAFO Divisions 3LMNO, 1991–1994.

Environmental factors were correlated with trends in relative abundance of both grenadier species. DFA found the NAO winter index and salinity at high lags were highly related to trends for two of the indices. The NAO index, the atmospheric pressure differential between the Azores and Iceland, exerts a strong influence over the ocean and atmosphere of the North Atlantic Ocean. The NAO influences sea ice extent and rate of melt, water temperature, the distribution and fluxes of major water masses and currents,

deep water formation in the Greenland Sea and intermediate water formation in the Labrador Sea (Hurrell et al. 2003). The index has risen steadily since the mid-1960s with decadal peaks in the early 1970s, 1980s and 1990s (Drinkwater 2002); a positive NAO index is associated with negative salinity anomalies, sea ice anomalies, and temperature anomalies (Marsden et al. 1991, Colbourne et al. 1997, Belkin et al. 1998, Belkin 2004). Negative salinity anomalies not only result in lower temperatures and a freshening of the upper waters, but also an intensification of stratification and restricted heat and nutrient exchange with deep waters (Blindheim and Skjoldal 1993), thereby affecting primary production in surface waters and ultimately food availability. In addition, salinity anomalies have been linked to sea ice anomalies (Marsden et al. 1991), cooling and freshening the North Atlantic deep-water (Brewer et al. 1983, Aagaard and Carmack 1994), and changing ocean-scale current patterns (Belkin et al. 1998).

I have shown, using several methods and various filterings of data sets ranging from comprehensive inclusion to statistically rigorous approaches, that *Coryphaenoides rupestris* and *Macrourus berglax* have declined in abundance in the northwest Atlantic (see also Devine et al. 2006). MAFA and DFA methods allow for testing for relationships between time series for these two species and a variety of explanatory variables. There was no one factor directly responsible for the declines; however, total grenadier catches, Greenland halibut catches, and a large-scale, basin-wide atmospheric condition, the NAO winter index, have been shown to be key factors related to the trends. These factors are operating on different spatial and temporal scales. Populations of deep-sea species decline dramatically under light exploitation and continued fishing, and species with extreme life-history characteristics will continue to show the effects of overfishing for several

generations (Koslow et al. 2000). The possibility exists that species with extreme life history characteristics may never recover from severe exploitation (Atkinson 1995, Roberts 2002).

The observed dramatic declines in abundance are partially the result of the life-history and ecological characteristics of the two North Atlantic grenadier species. Grenadiers show many of the characteristics typical of deep-sea species; they are slow-growing, late-maturing, long-lived, and have low fecundity (Merrett 1994, Moore and Mace 1999, Koslow et al. 2000, Clark 2001). Clarke et al. (2003) found *C. rupestris* displayed slow growth in the Northeast Atlantic; K, the Brody growth coefficient from the von Bertalanffy growth model, was 0.1 yr^{-1} for females and 0.13 yr^{-1} for males. *Macrourus* also displays slow growth; Murua (2003) estimated average rates (K) in NAFO Divisions 3LMN of approximately 0.13 yr^{-1} for males and 0.04 yr^{-1} for females. *Gadus morhua* in the Irish Sea and herring *Clupea harengus* in the Celtic Sea display much higher growth, estimated average rates are 0.43 yr^{-1} and 0.56 yr^{-1} respectively (Clarke et al. 2003). Maximum age attained from survey samples in the Northeast Atlantic for *C. rupestris* was 60 years for females and 50 years for males (Clarke et al. 2003), maturation is at age 11 and a modest number, <57,000, of large eggs are produced (Alekseyev et al. 1992, Kelly et al. 1997), attributes characteristic of species in low-energy environments (Ekau 1991). In the Northwest Atlantic, maximum age of *Macrourus* from catch data is 20 years, maturation is at approximately age 15 (Murua 2003, Costas and Murua 2005), similar to *Macrourus* in the northeast Atlantic (Eliassen and Falk-Petersen 1985), and the amount of eggs spawned ranges between 8500–62,000 (Savvatimsky 1994, Murua 2003, Savvatimsky and Gorchinsky 2001). Both sexes of *M. berglax* are fully recruited to the

fishery at age 8 (Savvatimsky and Gorchinsky 2001, Murua 2003). Mortality rates (Z) for the Flemish cap range between 0.29–0.47 yr^{-1} for females and 0.59–0.69 yr^{-1} for males based on both survey and commercial data (Murua 2003).

Savvatimsky and Gorchinsky (2001) hypothesized that *Macrourus berglax* in NAFO Divisions 0B2GHJ3KLMN are a single stock based on size-age composition, although the isolation of the Flemish Cap from the Grand Banks by the cold waters of the Labrador Current render this conclusion questionable. Using parasites as natural tags allows for identification of distinct populations of fishes, especially in the deep-sea where parasite diversity decreases with distance from the continental slope (Kabata 1963, Templeman and Fleming 1963, Campbell et al. 1980). Analysis of parasites has shown that fish species, including *Macrourus,* on the Flemish Cap host a different suite of parasites than species from the Newfoundland Shelf and Grand Banks (Zubchenko 1981, Campbell 1983).

Life-history of the grenadier species must be considered when attempting to develop management objectives. Because of the longevity of deep-sea species, any disturbance to the community may take many years to be noticed (Koslow et al. 2000), unlike many pelagic or shelf species that are r-selected and can react quickly to changing conditions (Bakun 1986, Jørgensen 2002). The time scale over which deep-sea species have been studied is short, and often not even begun before a directed fishery has peaked and collapsed (Atkinson 1995, Haedrich et al. 2001, Roberts 2002). Compounding problems are the difficulties in attempting to determine whether changes are primarily a result of the environment or overfishing. It is often easy to claim overfishing as the main cause for change. Here I have shown that, indeed, fishing pressure is a main factor explaining

trends in *Coryphaenoides rupestris* and *Macrourus berglax,* however, large-scale atmospheric conditions that operate across the North Atlantic also play a role. These populations are not virgin stocks, but have experienced several decades of intense exploitation, especially *Coryphaenoides*. Stocks already changed and weakened by overfishing are often more susceptible to the effects of changing environment (Pauly and Maclean 2003).

I have shown that MAFA and DFA can describe dynamics of single populations (Chapter 3) and deep-sea species, which are rarely the focus of long-term research programs. The next obvious step is to determine if dynamics of a community can be described.

Table 6.1. Results of generalized linear models for the four relative abundance metrics (weighted number per tow) and adult abundance (number per tow), number of data points used to generate the estimate, estimated exponential decline (%) and 95% confidence interval of the decline (%) for *Macrourus berglax* and *Coryphaenoides rupestris* in Canadian waters of the Northwest Atlantic 1978–2003. Note: -- indicates the confidence interval encompassed 0.

Macrourus berglax	All Data	Fall Only	Consistent Strata	Fall, Consistent Strata	Adults-only
AIC	0.0019	0.0044	0.0029	0.0094	1.4239
Year	-0.0167	-0.0273	-0.0811	-0.0863	-0.0290
Year SE	0.0334	0.0327	0.0380	0.0343	0.0023
Strata	0.0017	0.0011	0.0028	0.0019	0.0001
Strata SE	0.0012	0.0011	0.0016	0.0013	0.0001
Intercept	0.8785	2.4887	6.1810	7.6260	1.3235
Intercept SE	2.9764	2.8718	3.3423	3.0087	0.1944
n data points	43802	21767	27137	10800	5212
Decline (%)	35.2	49.5	87.8	88.5	55.7
95% CI (%)	-- – 88.2	-- – 89.8	15.6 – 98.2	38.0 – 97.8	49.8 – 60.8
Coryphaenoides rupestris					
AIC	0.0026	0.0057	0.0029	0.0092	5.8232
Year	-0.0740	-0.0852	-0.1568	-0.1638	-0.2024
Year SE	0.0309	0.0307	0.0446	0.0383	0.0028
Strata	0.0005	0.0002	0.0038	0.0027	0.0001
Strata SE	0.0008	0.0008	0.0016	0.0013	0.0001
Intercept	7.3042	8.8100	12.3901	14.0549	21.1606
Intercept SE	2.7235	2.6982	3.8705	3.3297	0.2708
n data points	43802	21767	27137	10800	1672
Decline (%)	85.4	88.1	98.3	98.3	99.7
95% CI (%)	29.6 – 97.0	46.5 – 97.4	83.5 – 99.8	89.1 – 99.7	99.6 – 99.7

Table 6.2. Most significant correlations between MAFA axes and explanatory factors, including lags, for three indices of relative abundance for *Macrourus berglax* and *Coryphaenoides rupestris* in the Northwest Atlantic, 1978–2003. Significance level for correlations = 0.39, adult index significance = 0.38. See text for abbreviations of factors, number appended to the factor indicates the lag in years.

All Data		Consistently Sampled Strata			Adults-only	
Factor	MAF1	Factor	MAF1	MAF2	Factor	MAF1
BT 4	-0.50	BT 0	**0.64**	-0.01	BT 0	0.72
Catch 17	-0.54	BT 11	0.35	**0.42**	Catch 7	0.61
GHCt 15	-0.64	Catch 6	**0.78**	0.11	GHCt 17	-0.67
NAO 0	-0.56	GHCt 9	-0.11	**-0.51**	NAO 9	-0.64
SAL 5	-0.50	GHCt 18	**-0.79**	0.00	SAL 1	0.74
SST 2	0.57	NAO 14	**-0.59**	**-0.52**	SST 0	-0.50
		SAL 1	**0.56**	0.14		
		SAL 12	**0.39**	**0.45**		
		SST 4	0.02	**-0.57**		
		SST 14	**0.54**	0.15		

Table 2. Values of Akaike's information criterion (AIC) for DFA models and different sets of explanatory variables (exp), based on a diagonal covariance matrix. The number appended to the explanatory variable indicates the time lag in years. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
All data		
Relative abundance + noise		
1 trend model	–	118.3
2 trend model	–	117.2
Relative abundance + exp + noise	Grenadier catch 15	120.8
	Greenland halibut catch 1	114.7
1 trend model	Grenadier catch 15 + Greenland halibut catch 1	105.5
2 trend model	Grenadier catch 15 + Greenland halibut catch 1	**102.1**
Consistently sampled strata		
Relative abundance + noise	–	94.4
Relative abundance + exp + noise	Greenland halibut catch 1	86.4
	NAO index 14	80.6
1 trend model	Greenland halibut catch 1 + NAO index 14	**75.6**
Adults-only		
Relative abundance + noise	–	97.4
Relative abundance + exp + noise	Greenland halibut catch 8	92.2
	Salinity 12	93.4
1 trend model	Greenland halibut catch 8 + salinity 12	**85.9**

Table 6.4. Estimated regression parameters (**D**), standard errors and t-values for DFA models of three indices of relative abundance for *Macrourus berglax* and *Coryphaenoides rupestris* in Canadian waters of the Northwest Atlantic, 1977–2004. The three indices are (1) all data, (2) consistently sampled strata only, and (3) adults-only. See Chapter 2 for an explanation of **D**.

	M. berglax	*C. rupestris*
(1) Grenadier catch lagged 15 years		
Estimated value (**D**)	0.03	0.40
Standard error	0.11	0.14
t-value	0.29	2.81
(1) Greenland halibut catch lagged 1 year		
Estimated value (**D**)	-0.54	-0.11
Standard error	0.18	0.23
t-value	-3.00	-0.50
(2) Greenland halibut catch lagged 1 year		
Estimated value (**D**)	-0.12	-0.48
Standard error	0.08	0.09
t-value	-1.48	-5.39
(2) NAO index lagged 14 years		
Estimated value (**D**)	-0.33	-0.13
Standard error	0.09	0.09
t-value	-3.84	-1.43
(3) Greenland halibut catch lagged 8 years		
Estimated value (**D**)	0.09	-0.23
Standard error	0.11	0.08
t-value	0.86	-2.96
(3) Salinity lagged 12 years		
Estimated value (**D**)	0.32	0.13
Standard error	0.10	0.06
t-value	3.23	2.04

Table 6.5. Factor loadings and canonical correlations between *Macrourus berglax* and *Coryphaenoides rupestris* and the trends for the best DFA models for consistently sampled strata and adults-only abundance in the Northwest Atlantic, 1977–2004.

		Consistently sampled strata
	Factor loadings	Canonical correlations
Macrourus	0.27	0.93
Coryphaenoides	0.20	0.85
		Adults-only
	Factor loadings	Canonical correlations
Macrourus	0.20	0.82
Coryphaenoides	0.23	0.95

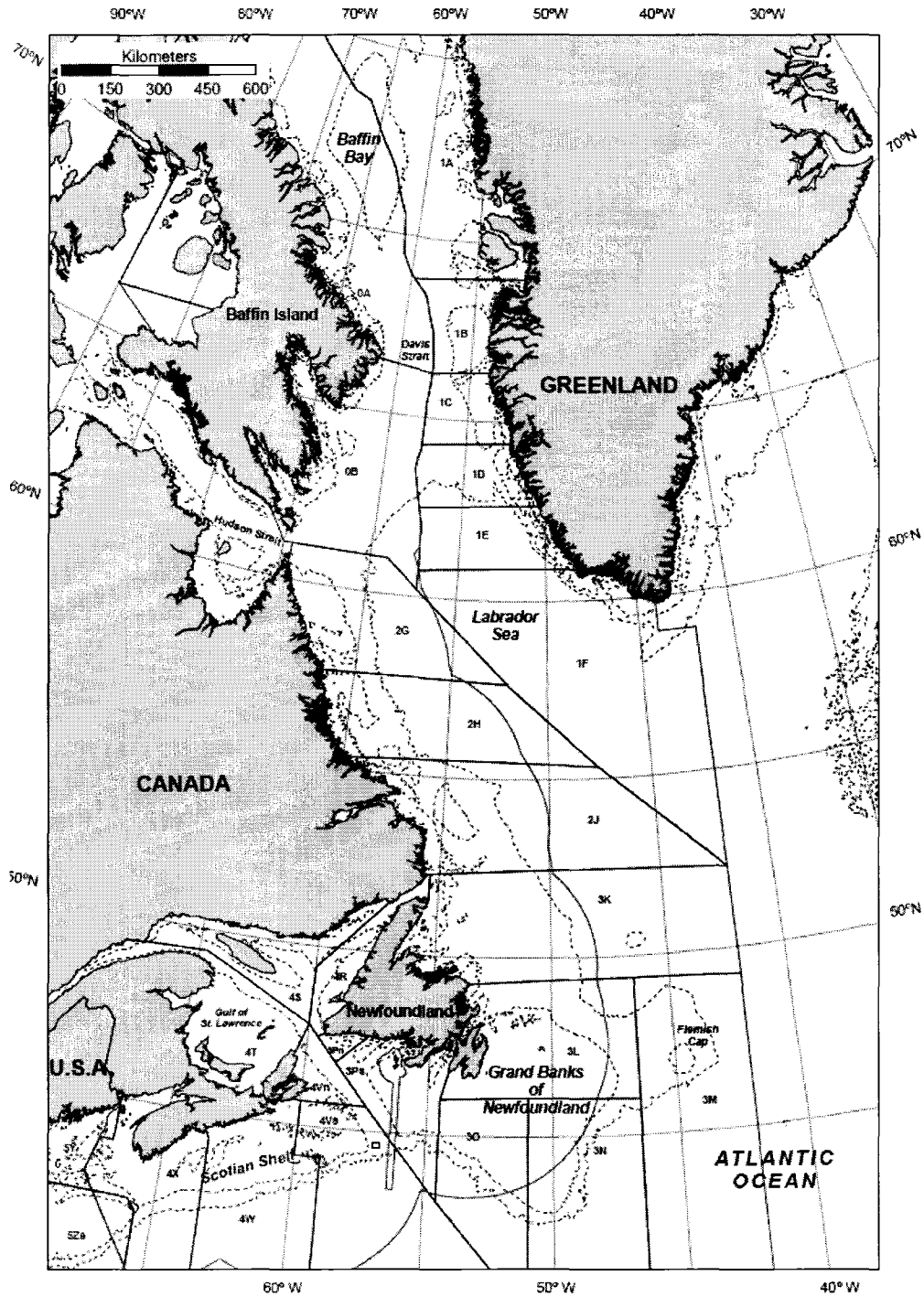

Figure 6.1. Canadian waters of the Northwest Atlantic, showing NAFO Divisions, location of the Canadian economic exclusion zone (200–mile limit, dashed line), and the 500 and 1000 meter bathymetric contours.

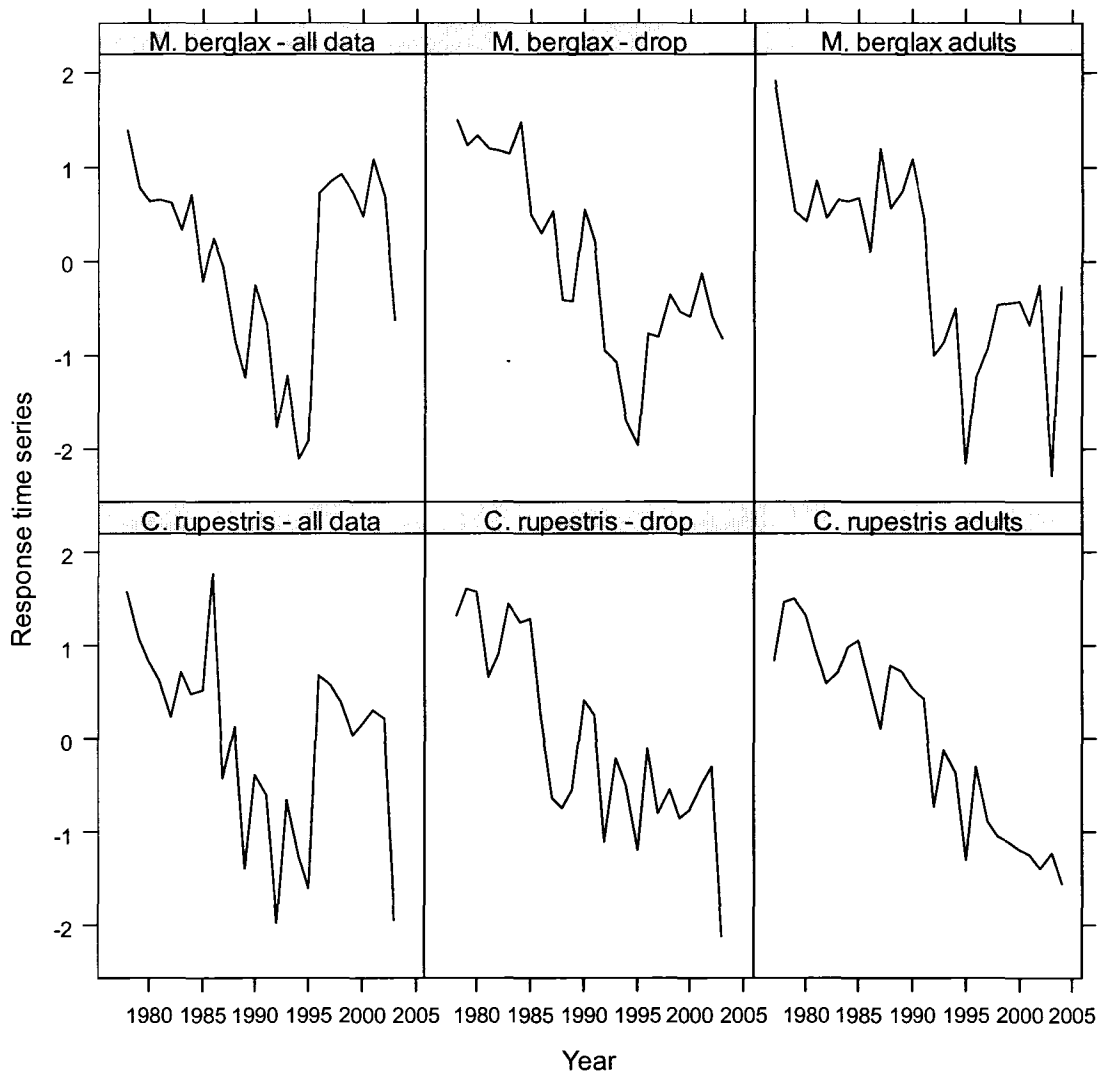

Figure 6.2. Relative abundance indices of *Macrourus berglax* and *Coryphaenoides rupestris* from Canadian waters of the Northwest Atlantic: all data (left), 1978–2003; consistently sampled strata (middle), 1978–2003; and adults–only (right), 1977–2004.

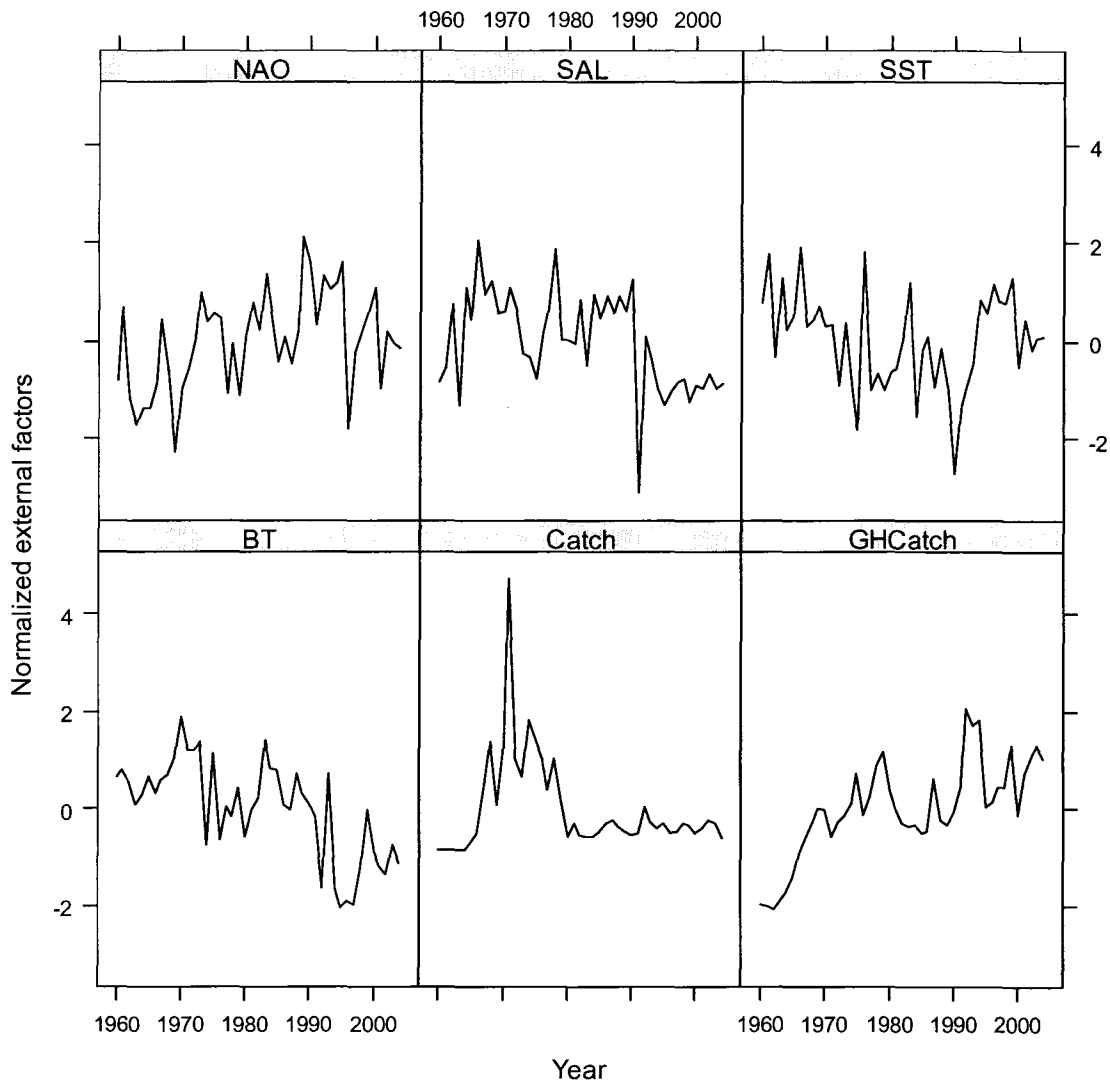

Figure 6.3. External factors included in MAFA and DFA, 1960–2004; variables are defined in the text (see Methods). NAO is the North Atlantic Oscillation winter index, SAL is salinity, SST is sea surface temperature, BT is bottom temperature, Catch is grenadier catch, GHcatch is Greenland halibut catch.

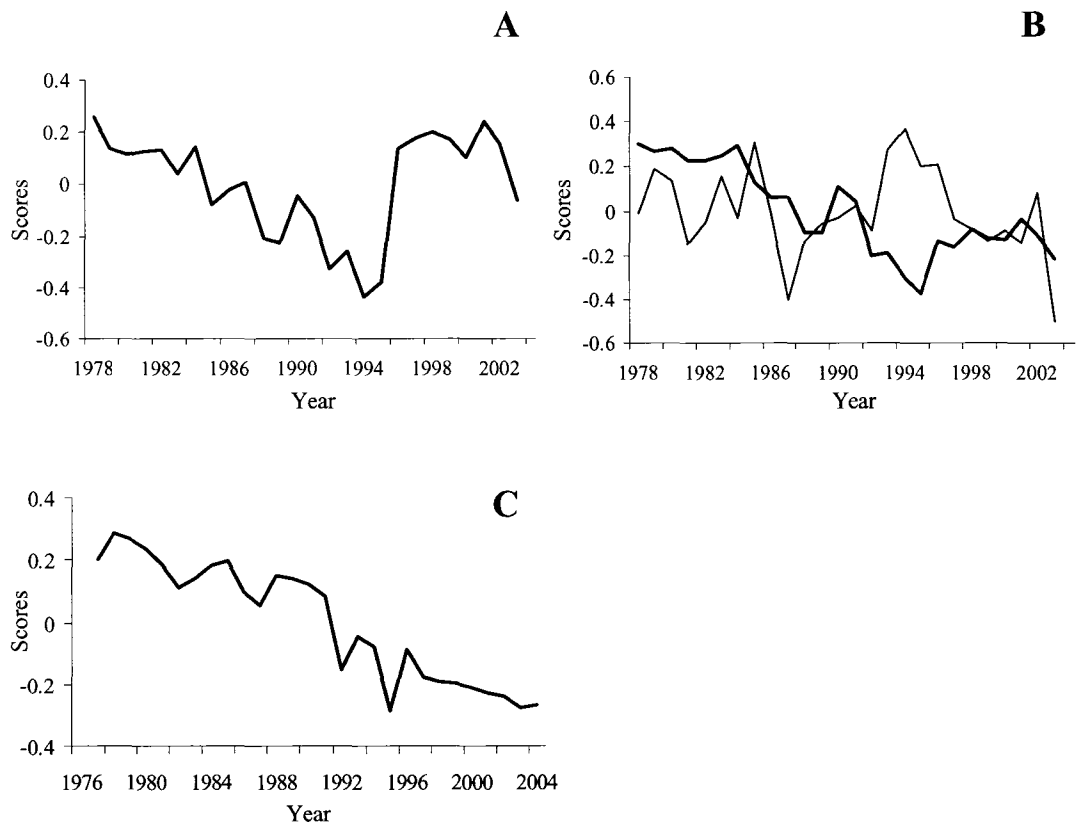

Figure 6.4. MAFA trends for three relative abundance indices for *Macrourus berglax* and *Coryphaenoides rupestris* in the Northwest Atlantic, 1978–2004: (A) all data, (B) consistently sampled strata, and (C) only adults. Heavy line signifies main trend, light line is the second trend.

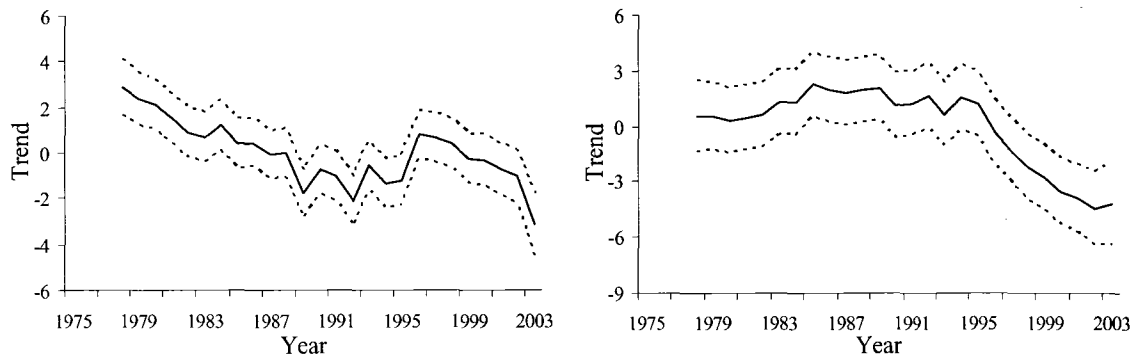

Figure 6.5. The (left) first and (right) second trends with confidence intervals for the DFA model with grenadier catch lagged 15 years and Greenland halibut catch lagged 1 year for relative abundance of *Macrourus berglax* and *Coryphaenoides rupestris* using all data from research surveys in Canadian waters of the Northwest Atlantic, 1978–2003.

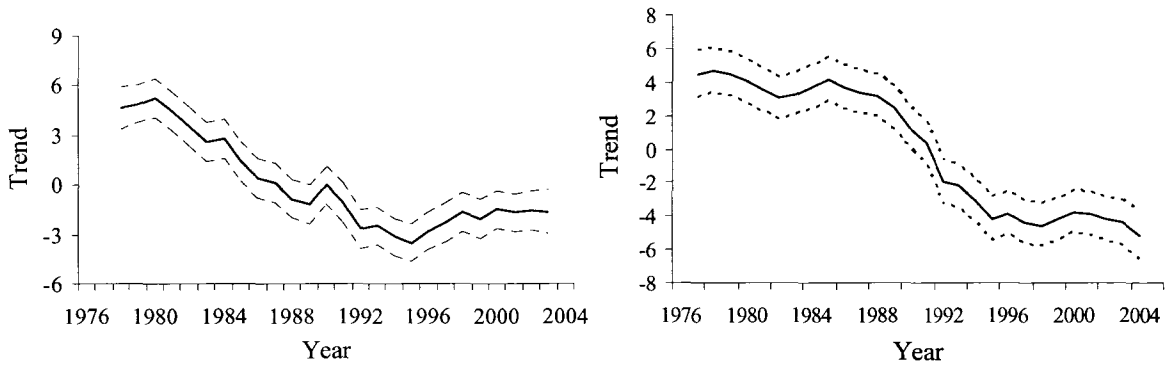

Figure 6.6. Main DFA trends with confidence intervals in *Macrourus berglax* and *Coryphaenoides rupestris* relative abundance using (right) consistently sampled strata from Canadian research surveys (all seasons), 1978–2003, and (left) adult relative abundance from Canadian autumn research surveys, 1977–2004.

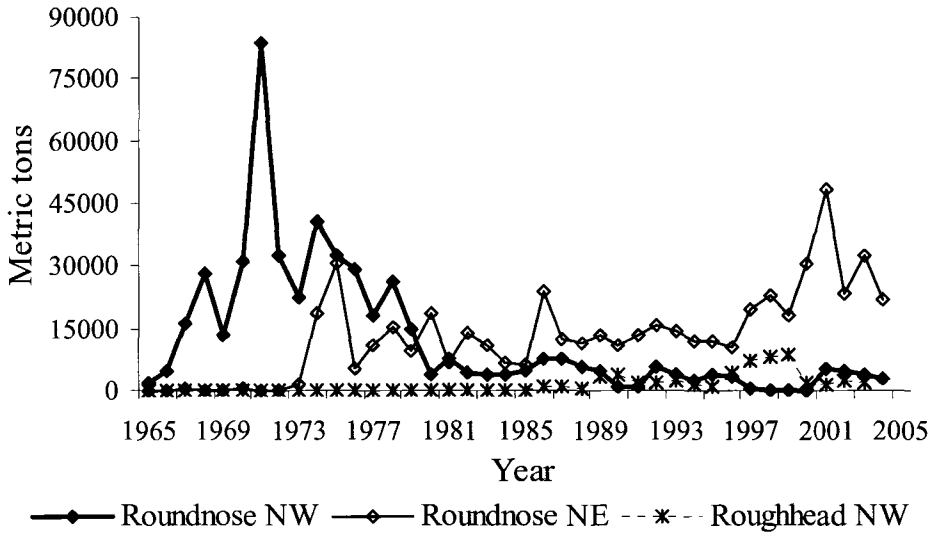

Figure 6.7. Grenadier, *Coryphaenoides rupestris* (roundnose) and *Macrourus berglax* (roughhead), landings in the North Atlantic, 1965–2004 (FAO statistics).

Appendix A. Raw data.

Table 1A. Time series of raw data for three indices of abundance (all data, consistently sampled strata, and adults-only) for *Coryphaenoides rupestris* and *Macrourus berglax*, 1977–2004.

	All data		Consistently sampled strata		Adults-only	
Year	*M. berglax*	*C. rupestris*	*M. berglax*	*C. rupestris*	*M. berglax*	*C. rupestris*
1977	–	–	–	–	1.15	37.21
1978	2.88	11.44	3.01	5.04	0.60	140.91
1979	1.86	5.79	2.47	7.68	0.32	147.19
1980	1.67	4.14	2.66	7.16	0.28	104.38
1981	1.70	3.14	2.43	1.96	0.43	44.96
1982	1.64	1.85	2.38	2.83	0.30	21.79
1983	1.33	3.62	2.33	6.07	0.35	28.43
1984	1.75	2.60	2.98	4.57	0.35	50.26
1985	0.89	2.72	1.46	4.75	0.36	59.16
1986	1.26	15.31	1.28	1.08	0.21	20.75
1987	1.01	0.75	1.50	0.30	0.59	7.89
1988	0.57	1.61	0.76	0.26	0.33	33.44
1989	0.43	0.20	0.75	0.35	0.39	28.30
1990	0.87	0.79	1.53	1.39	0.54	19.44
1991	0.65	0.58	1.20	1.09	0.29	15.51
1992	0.29	0.09	0.52	0.16	0.07	1.39
1993	0.43	0.55	0.47	0.56	0.08	5.01
1994	0.23	0.24	0.31	0.37	0.12	2.90
1995	0.26	0.15	0.25	0.14	0.02	0.41
1996	1.77	3.38	0.59	0.65	0.06	3.44
1997	1.95	2.97	0.58	0.24	0.08	0.98
1998	2.06	2.30	0.79	0.34	0.12	0.70
1999	1.79	1.41	0.70	0.23	0.12	0.64
2000	1.48	1.68	0.67	0.25	0.13	0.53
2001	2.29	2.05	0.94	0.37	0.10	0.46
2002	1.74	1.78	0.67	0.49	0.15	0.35
2003	0.66	0.09	0.57	0.04	0.02	0.48
2004	–	–	–	–	0.15	0.24

Table 2A. Time series of explanatory variables, 1960–2004. See Methods for abbreviations.

Year	BT	Catch	SST	SAL	NAO	Ghcatch	BT
1960	0.11	0	0.14	-0.07	-1.54	2546	0.11
1961	0.16	0	0.37	0.08	1.80	2158	0.16
1962	0.08	0	-0.13	0.65	-2.38	597	0.08
1963	-0.09	0	0.26	-0.29	-3.60	4555	-0.09
1964	-0.02	0	0.01	0.81	-2.86	7138	-0.02
1965	0.11	1800	0.07	0.52	-2.88	13203	0.11
1966	-0.01	4700	0.41	1.25	-1.69	22369	-0.01
1967	0.09	17310	0.02	0.74	1.28	29264	0.09
1968	0.13	31547	0.06	0.87	-1.04	35087	0.13
1969	0.24	12847	0.12	0.58	-4.89	39946	0.24
1970	0.54	30408	0.02	0.59	-1.89	39845	0.54
1971	0.30	79577	0.03	0.81	-0.96	28897	0.30
1972	0.31	26697	-0.26	0.60	0.34	34854	0.31
1973	0.36	21394	0.04	0.19	2.52	37467	0.36
1974	-0.37	38073	-0.30	0.17	1.23	42169	-0.37
1975	0.28	32174	-0.49	-0.04	1.63	53897	0.28
1976	-0.34	26486	0.39	0.38	1.37	37705	-0.34
1977	-0.10	17600	-0.29	0.60	-2.14	44946	-0.10
1978	-0.18	26541	-0.21	1.18	0.17	57046	-0.18
1979	0.02	14597	-0.29	0.33	-2.25	62058	0.02
1980	-0.31	3774	-0.20	0.31	0.56	46974	-0.31
1981	-0.13	7477	-0.19	0.28	2.05	40121	-0.13
1982	-0.04	4392	-0.05	0.70	0.80	34156	-0.04
1983	0.38	3591	0.24	0.09	3.42	33181	0.38
1984	0.17	3898	-0.42	0.75	1.60	33620	0.17
1985	0.16	4987	-0.09	0.53	-0.63	30380	0.16
1986	-0.09	7513	-0.03	0.73	0.50	30935	-0.09
1987	-0.12	8675	-0.28	0.58	-0.75	51904	-0.12
1988	0.13	6740	-0.08	0.73	0.72	35518	0.13
1989	-0.01	5053	-0.28	0.60	5.08	34030	-0.01
1990	-0.07	4241	-0.70	0.89	3.96	38758	-0.07
1991	-0.17	4884	-0.36	-1.12	1.03	48662	-0.17
1992	-0.68	12300	-0.28	0.36	3.28	79076	-0.68
1993	0.14	7973	-0.16	0.17	2.67	73060	0.14
1994	-0.70	6374	0.15	-0.13	3.03	74810	-0.70
1995	-0.83	7615	0.09	-0.29	3.96	40616	-0.83
1996	-0.78	4814	0.22	-0.17	-3.78	43011	-0.78
1997	-0.81	5005	0.15	-0.07	-0.20	48502	-0.81
1998	-0.54	7426	0.14	-0.03	0.72	48667	-0.54
1999	-0.13	7296	0.26	-0.26	1.70	65142	-0.13
2000	-0.43	4918	-0.17	-0.11	2.80	37925	-0.43
2001	-0.53	6251	0.05	-0.13	-1.89	53935	-0.53
2002	-0.60	8573	-0.09	0.00	0.76	60072	-0.60
2003	-0.38	7800	-0.04	-0.14	0.20	65251	-0.38
2004	-0.50	3182	-0.03	-0.09	-0.07	59753	-0.50

Appendix B. Model fits for DFA models.

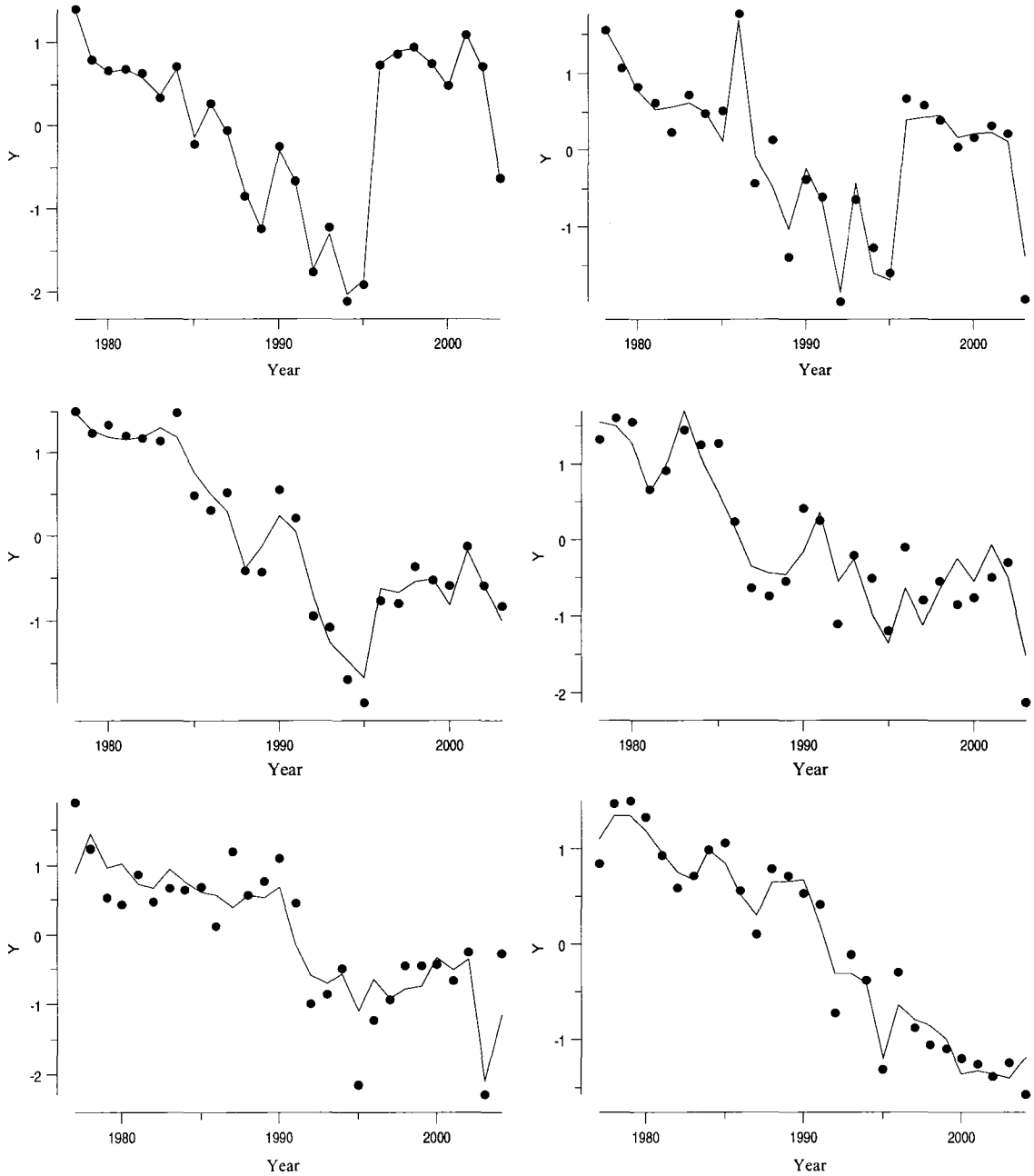

Figure 1B. Observed (points) and fitted (line) abundance for the best DFA models for *Macrourus berglax* and *Coryphaenoides rupestris* from all data (top row; 2-trend, 2-explanatory variable model), consistently sampled strata (middle row; 1-trend, 2-explanatory variable model) and adult-only data (bottom row; 1-trend, 2-explanatory variable model) from Canadian waters of the Northwest Atlantic, 1977–2004.

[6]Chapter 7. Between the Devil and the Deep Blue Sea: Complex Dynamics in Demersal Communities

> I believe that the cod fishery, the herring fishery, pilchard fishery, the mackerel fishery, and probably all the great sea fisheries are inexhaustible: that is to say that nothing we do seriously affects the numbers of fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless.
>
> – Thomas Huxley (1884)

The Newfoundland and Labrador Shelf system once supported one of the world's greatest fisheries. Today, many of the stocks on the shelf have been devastated. Annual landings of all groundfish species declined rapidly in 1978, stabilised in the 1980s, and then declined sharply again in the early 1990s (Boreman et al. 1997). Many groundfish fisheries, including Atlantic cod *Gadus morhua,* were closed in 1992. Changes in abundance, mean size and biomass are not restricted to commercial species; non-commercial species have also declined (Gomes et al. 1995, Haedrich and Barnes 1997, Bianchi et al. 2000, Zwanenburg 2000). As groundfish populations were declining, snow crab *Chionoecetes opilio*, northern shrimp *Pandalus borealis,* American lobster *Homarus americanus* and seal (*Phoca groenlandica* and *Cystophora cristata)* populations in the northwest Atlantic were steadily increasing (Lilly et al. 2000, Worm and Myers 2003, Hammill and Stenson 2005). Changes in energy flows and predation have been suggested

[6] Some material contained in this chapter has been published in Devine et al. 2007. *Complex dynamics in demersal communities on the Newfoundland-Labrador Shelf* pp. 601-612. *In* Zuur, A.F., Ieno, E.N. and Smith, G.M. (eds.) The Analysis of Ecological Data, Springer, and in Devine, J.A. and Haedrich, R.L. 2004. *Trends in fish populations in the northwest Atlantic*, pp.15-22. *In* Freitas, C.E. de C., Petrere, Jr., M. Rivas, A.A.F., and MacKinlay, D (eds.) Fish communities and Fisheries, Symposium proceedings of the International Congress on the Biology of Fish, Manaus, Brazil, August 1-5, 2004.

as hindering the rebuilding of some important commercial stocks (Barkai and McQuaid 1988, Walters and Kitchell 2001, Morissette et al. 2006).

The Newfoundland-Labrador Shelf has experienced varying environmental conditions. Temperatures were below average in the mid-1980s to mid-1990s (Drinkwater 2002). In the early 1990s, temperature anomalies in sea surface waters (0–176 meters) were the lowest since 1950 (Drinkwater 2002). Great salinity anomalies (GSAs) also occurred in the early 1970s, 1980s and 1990s and may be linked to changes in the North Atlantic Oscillation (NAO) (Belkin 2004). The NAO, the atmospheric pressure differential between the Azores and Iceland, exerts a strong influence over the ocean and atmosphere of the North Atlantic Ocean. The NAO plays a role in sea ice extent and melt, water temperature, the distribution and fluxes of major water masses and currents, deep water formation in the Greenland Sea, and intermediate water formation in the Labrador Sea (Hurrell et al. 2003).

Overfishing, predation, changes in prey availability, and environmental factors have all been pinpointed as possible causes for the observed declines in size and abundance of demersal fish species. A long, ongoing debate continues concerning which of the many possibilities has played the greatest role (NRC 1999, Hamilton et al. 2004). Examinations have ranged from the descriptive (e.g. Villagarcía et al. 1999) to the broadly analytical (e.g. Bianchi et al. 2000) and from the application of local ecological knowledge (e.g. Neis et al. 1999) to quantitative ecosystem models based in theory (e.g. Murillo 2001). Most studies have employed traditional analytical approaches that are limited in their scope and depend on key assumptions. Furthermore, the great majority of these studies have focused on only one species, Atlantic cod, with little or no consideration of other

species in the system. As would be expected, conclusions range across the spectrum as to principal causes, but there is general agreement that the situation is complex with underlying dynamics operating at a number of spatial and temporal scales.

My objective here is to determine whether the complex dynamics involving relative abundance and mean size of the Newfoundland-Labrador Shelf demersal community can be described using multivariate time series analysis. I used min/max autocorrelation factor analysis (MAFA) and dynamic factor analysis (DFA) (see Chapter 2) to analyse trends in relative abundance and mean size of commercial and non-commercial species and to examine relationships with external factors.

7.2. Methods

7.2.1. Study area

The Newfoundland-Labrador Shelf is a unique ecosystem because of its topography and circulation patterns (Figure 7.1). The shelf is broad, ranging from 150 to 400 km wide, overlain by polar waters and comprises the deepest shelf region off eastern North America (Helbig et al. 1992, Drinkwater and Mountain 1997). The Labrador Shelf topography is very complex; the shelf contains numerous shallow banks separated by deep saddles that provide channels from the deep-sea to the inner shelf and allow cross-shelf current exchange (Drinkwater and Harding 2001). Inner basins on the Labrador Shelf reach maximum depths of approximately 800 meters (Drinkwater and Mountain 1997). The northeast Newfoundland Shelf is broader and contains many deep bays inshore; offshore, the shelf is separated into flat banks broken by a basin that deepens to 500 meters. To the south, the shelf forms the shallow Grand Banks of Newfoundland, a

relatively flat area with an average depth of 80 meters (Helbig et al. 1992). The Labrador Current forms two distinct branches over the Newfoundland-Labrador Shelf. The main branch flows offshore along the continental slope centred at the 500 meter isobath, carries approximately 85% of the total transport and has surface currents up to 50 cm s^{-1}. The inshore branch flows along the inner half of the shelf with surface speeds up to 15 cm s^{-1} (Lazier and Wright 1993, Drinkwater and Harding 2001). The Labrador Current forms the cold intermediate layer (CIL), capped above and below by warmer waters, which affects the distribution and migratory patterns of many fish species.

7.2.2. Data

The ECNASAP (East Coast North American Strategic Assessment Project) dataset was used as the source of records for the Newfoundland-Labrador Shelf (NAFO Divisions 2J3KL) for the years 1978 through 1994 (see Brown et al. 1996 and Doubleday and Rivard 1981 for survey details). This database consists of data for each species (numbers and weights) taken in stratified random survey tows, where stratum boundaries are determined by depth. Prior to 1978, the survey was not based on a stratified random design and gear configuration varied (Doubleday 1981). Only strata consistently sampled over the 17-year time period were included; strata were included if they were sampled at least half of the time period (eight years) and at least twice during the first and last five years.

Data after 1994 were not used because of several changes in the sampling protocols employed in the Newfoundland-Labrador region, most importantly modifications to the survey design to include deeper waters and a gear change from an Engels 145 bottom

trawl to a Campelen 1800 bottom trawl. Catchability differs greatly between the two gears and gear comparison studies are needed to generate conversion ratios for individual species; however, these comparisons were done for only a few important commercial species (e.g. Stansbury 1997, Warren et al. 1997). One method of accounting for the gear change, as used in previous chapters, is to scale Campelen to Engels catches using species-specific scaling factors. This approach was not used here because permission could not be obtained from DFO to use available data from 1995 to present. Brodie (2005) cautioned that temporal and spatial restrictions since the gear change have introduced uncertainty into the survey estimates for some species. The ECNASAP data used, however, were from years that encompassed a period of drastic changes on the northern Newfoundland-Labrador Shelf. In addition, the ECNASAP data were subjected to rigorous scrutiny to ensure the data were comparable and they were vetted by an international group of fisheries biologists and taxonomists (Brown et al. 1996); data from 1995 onwards were not.

A mixture of important commercial, non-commercial and rare demersal teleost and elasmobranch species were chosen for the analysis, including: American plaice *Hippoglossoides platessoides* (AP), Atlantic cod *Gadus morhua* (AC), Atlantic wolffish *Anarhichas lupus* (AW), black dogfish *Centroscyllium fabricii* (BD), blue hake *Antimora rostrata* (BH), deepwater redfish *Sebastes mentella* (DR), golden redfish *Sebastes marinus* (GR), Greenland halibut *Reinhardtius hippoglossoides* (GH), northern wolffish *Anarhichas denticulatus* (NW), roughhead grenadier *Macrourus berglax* (RHG), roundnose grenadier *Coryphaenoides rupestris* (RK), spotted wolffish *Anarhichas minor* (SW), spinytail skate *Bathyraja spinicauda* (SS), and thorny skate *Raja radiata* (TS).

Indices used were mean weight per fish (kg per individual) and weighted number per tow, an index of relative population abundance where data were weighted by the area of the stratum (square nautical miles). Changes in mean weight per fish combined two trends: changes in size-at-age and the disappearance or appearance of large, old fish (Hamilton et al. 2004). Relative abundance was $\log_{10}$ transformed and both indices were standardized to a zero mean and unit standard deviation. Raw data can be found in Appendix C.

Seven external factors were used, including five environmental variables, one measure of exploitation, and one measure of potential natural predation. Mean sea surface temperatures (SST) from NAFO Divisions 2J3KL from 1960–1994 at 0–100 meters were used with the CIL, defined as waters deeper than 30 meters and less than 0° Celsius (Drinkwater 1996), excluded. Two measures of bottom temperature from 1960–1994 were used from NAFO Divisions 2J3KL, shallow 250–500 meters (BTsh, of bottom temperature shallow) and deep 500–1485 meters (the maximum survey depth, BTdp or bottom temperature deep). Salinity (SAL) 1960–1994 was taken from NAFO Divisions 2J3KL at 0–250 meters depth based on Dickson et al. (1988), who found the effect of Great Salinity Anomalies (GSAs) on Newfoundland-Labrador shelf and eastern Grand Banks extended to approximately 300 meters. The NAO winter index (NAOW) was also included (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) for each year. Exploitation was fishing effort (EFF), number of days fished for all groundfish species, obtained from the NAFO fisheries statistics database (www.nafo.ca). The measure of possible predation was harp seal abundance (HARP), obtained from the Department of Fisheries and Oceans (DFO), Newfoundland-Labrador Region. Abundance was used as a rough estimate of possible predation pressure; as seal abundance increases, predation pressure should also

increase and vice versa. All explanatory factors were standardized by normalization. Raw data can be found in Appendix C.

7.2.3. Time series analysis

Cross-correlations determined whether lags were important between response and explanatory variables. MAFA and DFA were presented in detail in Chapter 2, and other examples of their use appear in Chapters 3 and 6. The methodology is the same, and therefore I omit description of the technique here.

7.3. Results

Strict statistical rigor was employed at the risk of losing some information. Specifically, restricting the analyses to consistently sampled strata resulted in the loss of 380 tows out of 11,833 over the 17-year time period. This filtering also eliminated some deep-water data. The original depth sampled was 42–1485 m, but after filtering the depth range of the tows was 42–1100 m. Time series of response and explanatory variables are shown in Figure 7.2.

7.3.1. Time series and correlations

Cross-correlations between response variables and explanatory variables at lags up to 18 years showed many lagged explanatory variables had higher correlations than variables with no lags (matrices have not been included here due to their size, but are available on request). This result confirmed the need to include lagged variables in the analyses.

7.3.2. MAFA analysis

MAFA analysis indicated no significant trends in relative abundance of the fourteen species, but two trends were highly autocorrelated (MAF1 autocorrelation = 0.99, p=0.106; MAF2 autocorrelation = 0.88, trend not significant, Figure 7.3a). The first trend was a steady decline over time. The second trend indicated stability until 1984, an increase through 1987 and then a decline. Canonical correlations between the species time series and MAFA axes indicated that the main trend was related to all species except Greenland halibut (Figure 7.3b), whereas the second trend was important only for Atlantic cod; all significant correlations were positive (Figures 7.3c). Significance level for all correlations was $r^2 \geq 0.49$.

Analysis of mean size (kg per individual) indicated that although no trends were significant, three trends were highly autocorrelated at time lag 1 (MAF1 autocorrelation= 0.97, p=0.42; MAF2 autocorrelation = 0.92, trend not significant; and MAF3 autocorrelation = 0.76, trend not significant). The first trend indicated stability until 1985 followed by a decline (Figure 7.4a). This trend was significantly and positively correlated with Atlantic cod, Atlantic wolffish, black dogfish, blue hake, Greenland halibut, roughhead grenadier, spinytail skate, spotted wolffish and thorny skate (Figure 7.4b); a correlation greater than 0.49 was significant at the 5% level for all species. The second trend was an increase from 1980 to 1987 and then a steep decline (Figure 7.4a). This trend was significantly and positively correlated with American plaice, deepwater redfish, northern wolffish, roughhead grenadier, and spotted wolffish (Figure 7.4c); significance level for correlations ≥ 0.49 for all species. The third trend was an oscillation with peaks

in 1980 and 1990 and minima in 1986 and 1994 (Figure 7.4a); this trend was significantly and positively correlated with deepwater redfish, northern wolffish, and rock grenadier (Figure 7.4d). No trends in mean size were significantly or even highly correlated with golden redfish. Significance level for all correlations was $r^2 \geq 0.49$.

Because 133 explanatory variables and lags were used, only the most significant correlations for each factor are presented for each analysis (Table 7.1); all correlations were significant at the 5% level if greater than or equal to 0.49. For relative abundance, all external factors at various lags were significantly related to the first trend, which was a decline over time. Salinity, the NAO index and predation, were negatively related, whereas the other four factors were positively related. Five factors were significantly correlated with MAF2; salinity, bottom temperature (shallow), predation, and exploitation were significantly and negatively correlated. Bottom temperature (deep) was significantly and positively correlated. All factors except effort were significantly correlated at low lags for MAF 1 and high lags for MAF2, effort was significantly correlated at high lags for MAF1 and low lags for MAF2. Out of 266 correlations (133 factors × 2 trends), 70 were estimated to be significantly different from zero at the 5% level, 14 of which could be expected by chance alone.

Salinity, NAO index, and predation at various lags were significantly and negatively correlated with the first trend in mean size, while both indices of bottom temperature and exploitation were significantly and positively related (Table 7.1). Significance level for all correlations was $r^2 \geq 0.49$. As with relative abundance, salinity, bottom temperature (shallow), predation, and fishing effort were significantly and negatively correlated with the second trend, whereas bottom temperature (deep) was significantly and positively

related with MAF2. Although the factors and sign of the correlation were similar for the first two trends with respect to both mean size and relative abundance, different lags were shown to be significant. Five factors were also significant for MAF3; both bottom temperatures, predation, and exploitation were positively related, while the NAO winter index was negatively related. Significance level for all correlations was $r^2 \geq 0.49$. Eighty correlations of 399 (133 factors × 3 trends) were significantly different from 0 at the 5% level; 20 could have been significant by chance alone.

7.3.3. DFA analysis

Akaike's Information Criterion (AIC) (Sakamoto et al. 1986) was used initially to determine the optimal model in terms of goodness of fit and the number of parameters; the model with the smallest AIC value was selected as being the best. Fitted values and residuals were also used to determine goodness of fit. Regression parameters and the diagonal and off-diagonal elements in the error covariance matrix were used to determine if additional explanatory variables and trends improved the model fit.

7.3.3.1. Relative abundance

DFA models with lagged explanatory variables gave a better fit than those with no lags. Models based on a symmetric, non-diagonal covariance matrix gave better fits than those based on a diagonal covariance matrix. The best model was the model with two common trends and two explanatory variables: fishing effort lagged 9 years and salinity lagged 11 years (1 common trend, AIC = 86.5; 2 common trends, AIC = 91.6). Although the one-trend model had a smaller AIC value than the two-trend model, the error

covariance matrix had larger diagonal and off-diagonal elements, indicating that there was residual information not explained in the one-trend model.

Common trends identified by DFA were not ranked in order of importance (Zuur and Pierce 2004), but their relative importance can be determined by comparison with MAFA trends. The two trends identified by DFA for relative abundance were very similar to the MAFA trends. The first DFA trend was a decline over time until 1987 and then a small increase (Figure 7.5a). Atlantic wolfish, blue hake and rock grenadier were strongly and positively related to the first trend; all other species were weakly related to the trend. Factor loadings showed that most species were positively related to the first trend except for Atlantic cod and Greenland halibut (Figure 7.5c). A decline in the trend is related to a decline in abundance if the factor loadings are positive. A negative relationship indicates abundance is increasing, i.e. the trend for the species is the opposite of what is suggested in the figure. The second trend was a small oscillation followed by a steep decline in 1989 (Figure 7.5b). Factor loadings indicated blue hake, rock grenadier and Greenland halibut were negatively related to the trend, whereas all other species were positively related (Figure 7.5c).

Estimated t-values for regressions for individual species show all species except Atlantic cod, golden redfish and thorny skate were strongly related with fishing effort lagged 9 years, as indicated by their high t-values (Table 7.2). Only Greenland halibut was strongly related with salinity lagged 11 years. The cross-correlation between the two explanatory variables was -0.49; this was high, but not significant. Diagonal elements of the error covariance model were relatively small (range -0.14 – 0.35, only two of 196 $\geq$ 0.3), indicating that the model fit the relative abundance time series well for all species.

The model with two trends and two explanatory variables improved the fit of the model compared to models with 0 or 1 explanatory variable, or only 1 trend (Table 7.3, Appendix 7A). Adding a second factor, salinity, to the model improved the fit for spotted wolffish, thorny skate, roughhead grenadier, rock grenadier, blue hake, Greenland halibut and Atlantic wolffish (Figure 7.6).

7.3.3.2. Mean size

Diagonal covariance models fit better than models based on a non-diagonal covariance error structure for mean size. Lagged explanatory variable models gave better fits than non-lagged models. The best model was not a three-trend model, as with the MAFA analysis, but a two-trend, two-explanatory model with harp seal abundance (predation) lagged 16 years and NAO index lagged 4 years (1 common trend, AIC = 499.7; 2 common trends, AIC = 440.5; 3 common trends, AIC = 446.3). The error covariance matrix for the two-trend model had only slightly larger diagonal elements than the three-trend model, indicating that adding a trend did not provide much more information. Additionally, the model fit to observed values was quite poor for the three-trend model compared to the two-trend model. One-trend, one-explanatory models did have lower AIC values; however, examination of the error covariance matrix showed there was a lot of residual information remaining (**I**, range 0.13–0.74).

The first trend identified by DFA was similar to the first MAFA trend for mean size; the trend declined from 1982 to 1989 and then remained at a fairly stable low level (Figure 7.7a). Factor loadings indicated only three species were negatively correlated with the first DFA trend: northern wolffish, roughhead grenadier and American plaice

(Figure 7.7c). The second trend was a slight oscillation, followed by a decline in 1991 and was very similar to the second MAFA trend for mean size (Figure 7.7b). All species except spotted wolffish were positively correlated with this trend; seven species were highly and positively correlated (factor loadings ≥ 0.32, Figure 7.7c).

Estimated t-values for regressions for individual species showed ten species had a strong relationship with predation lagged 16 years, as indicated by their high t-values (Table 7.4); those that did not have a strong relationship were Atlantic cod, black dogfish, golden redfish and rock grenadier. Four species, American plaice, deepwater redfish, golden redfish and northern wolffish, were strongly related with NAO winter index lagged 4 years. The cross-correlation between the two explanatory variables was 0.37, but the correlation was not significant (correlations ≥ 0.50 were significant at the 5% level). The model fit the mean size time series well for all species, as indicated by the relatively small diagonal elements of the error covariance model (**I** range 0 – 0.54, only one of 14 > 0.28). The 2-trend, 2-explanatory variable model improved the fit of the model compared to models with 0 or 1 explanatory variable, or only 1 trend (Table 7.5, Appendix 7B). Adding the NAO winter index to the model improved the fit for five species: thorny skate, northern wolffish, rock grenadier, deepwater redfish, Greenland halibut, and slightly improved the model fit for an additional four species: roughhead grenadier, spinytail skate, American plaice, and black dogfish (Figure 7.8).

7.4. Discussion

MAFA and DFA found similar trends in relative abundance and individual mean size for fourteen teleost and elasmobranch species on the northeast Newfoundland-Labrador

Shelf, 1978–1994. The main trend identified by both analyses was a decline over time, whereas the steepness of the decline varied depending on the particular index and analysis. Both types of analyses identified a mixture of external factors that were related to the trends, and included environmental, exploitation, and predation factors.

Population age-class structure and mean size-at-age for many commercial and non-commercial fish species captured in research surveys and commercial fisheries have declined since the early 1980s (Haedrich 1995, Bowering et al. 1997, Haedrich and Barnes 1997). Atkinson (1994) analyzed trends in demersal species from autumn bottom trawl surveys in 2J3KL 1981–1991 and found declines in biomass and abundance were evident in most species analyzed. Gomes et al. (1995) found similar changes in groundfish assemblages on the Northeast Newfoundland-Labrador Shelf (NAFO Divisions 2J3K); their deep assemblage declined beginning in the late 1970s whereas the northern assemblage experienced a slight increase to the mid-1980s, followed by a steep decline.

MAFA results showed that trends were correlated with most external factors, but the strongest correlations were with fishing effort, predation and bottom temperature from depths greater than 500m. A paucity of larger, older fish is primarily an effect of fishing effort (Hamilton et al. 2004), whereas an increase in smaller fish may be a sign that size-at-age is changing, resulting from both fishing and environmental changes (Bianchi et al. 2000). Deep bottom temperature, except for a low around 1984–1985, tended to follow the trajectory of the MAFA trends in relative abundance and mean size (increasing in the early 1980s and decreasing to lows after 1992). Changes in species abundance or size and temperature are often highly correlated (McGinn 2002) and temperature has been

suggested as causing large-scale distribution shifts and increased mortality in groundfish species (de Young and Rose 1993, Gomes et al. 1995, Drinkwater 2002 and references therein). There are an equal number of studies citing the role of high exploitation for the decreases in abundance and individual size (Haedrich and Barnes 1997 and references therein, Myers et al. 1997, Boreman et al. 1997). Mean weight, body condition, length and population size structure are often negatively correlated with increasing fishing effort, a sign of size selective exploitation (Pauly and Maclean 2003).

DFA results showed that salinity was an important variable for trends in relative abundance. Salinity, except for anomalies in the early 1980s and 1990s, was generally higher than average for most of the 1980s. Salinity anomalies have been proposed as being responsible for changes in sea ice (Marsden et al. 1991), changes in sea surface temperature (Dickson et al. 1988), cooling and freshening of the North Atlantic deep-water (Brewer et al. 1983, Aagaard and Carmack 1994), and changing ocean-scale current patterns (Belkin et al. 1998). Salinity anomalies not only result in lower temperatures and a freshening of the upper waters, but also in an intensification of stratification and restricted heat and nutrient exchange with deep waters (Blindheim and Skjoldal 1993), thereby affecting primary production in surface waters and food availability. Although Dickson et al. (1988) noted that the effects of salinity anomalies could be seen to 250–300m, their effects have been noted as deep as 1000 m in the northeast Atlantic (Edwards et al. 2002).

DFA results showed that lagged fishing effort or harp seal abundance (predation) was strongly related with the trends in relative abundance and mean size for most of the demersal species. Fishing effort has an immediate effect on populations by reducing the

number and size of fish present. However, it also has a cumulative effect, reducing the number of fish that will recruit to the population in the future. Fishing effort declined from 1970 until the mid-1980s and then increased until the closure of many fisheries in the early 1990s (Figure 7.2). Despite such action, these closures did not result in zero predation because the target species are captured as by-catch in other fisheries. As the groundfish fisheries were collapsing, fishermen turned to harvesting shrimp and crab. These two fisheries have some of the highest discard rates recorded. Ninety-eight percent of the by-catch from shrimp fisheries in the northwest Atlantic, which is mainly juveniles and sub-adult fish, is discarded (Alverson et al. 1994). Although fishing has an effect on all sizes of fish, harp seals have been shown to select a variety of size ranges including fish that have not yet recruited to the fishery (Stenson et al. 1997, Hammill and Stenson 2000, Morissette et al. 2006). Annual predation of juvenile redfish (< 25 cm) alone is estimated at 175 million individuals (Morin et al. 2004).

DFA results also indicated that the NAO index was important with respect to trends in mean size. It has long been understood that regional atmospheric processes are important factors that regulate change and are often better predictors of local, large-scale ecological processes than local weather, such as daily temperature (Klyashtorin 1998, Wilbanks and Kates 1999, Fréon et al. 2003, Sharp 2003, Hallett et al. 2004). A positive NAO is responsible for salinity, sea ice, and temperature anomalies (Marsden et al. 1991, Colbourne et al. 1997, Belkin et al. 1998, Belkin 2004), and of these, sea ice anomalies directly influence the timing and extent of harp seal migrations southward (Stenson et al. 1997). Greater southward extent of ice in the mid-1980s may have contributed to changes

in fish mean size as a result of the possibility of greater predation rates by seals, which are size-selective piscivores.

MAFA and DFA methods allowed testing for relationships between time series of the demersal community with a variety of explanatory variables. These analyses show predation, in general, has important effects on relative abundance and mean size of species. Many studies have described community changes that result from environmental changes and fisheries (a type of selective predation), but few have looked at predation by multiple causes. Predation is always present in marine systems and removals by natural predation can exceed removals by fisheries (Bax 1998). Seal predation has been shown to potentially consume large quantities of fish in Atlantic Canada (Shelton et al. 2006). But this is only one type of predation; consumption of fish by other fish can far exceed that of marine mammals (Morissette et al. 2006).

This analysis has illustrated an objective technique to gain insight into the elements of a changing system, and is unique in being based on fisheries independent data while also including the potential effects of a natural, non-human predator. These techniques and their results highlight the complexity of the Newfoundland-Labrador Shelf ecosystem; many dynamics occur at the same time, often within populations of the same species, but their rates and interactions vary temporally and spatially. No one factor is responsible for the changes that are taking place. Biological and environmental factors, acting in combination at different temporal scales, have resulted in the dramatic changes seen today.

Table 7.1. Most significant correlations between MAFA axes and each type of explanatory factor at various lags for relative abundance and mean size of fourteen species in the Northwest Atlantic, NAFO Divisions 2J3KL, 1978–1994. Significance level for all correlations is 0.49. For factor codes, see text. Numbers after the factor codes indicate the time lag in years.

	Relative Abundance			Mean Size		
Factor	MAF1	MAF2	Factor	MAF1	MAF2	MAF3
SAL9	**-0.62**	0.31	SAL10	**-0.64**	0.13	0.04
SAL16	-0.09	**-0.54**	SAL14	-0.14	**-0.59**	0.22
SST2	**0.50**	0.09	BTsh3	0.38	0.21	**0.59**
BTsh2	**0.60**	0.29	BTsh13	0.40	**-0.51**	0.33
BTsh15	0.49	**-0.55**	BTsh16	**0.60**	-0.15	-0.46
BTdp2	**0.85**	0.01	BTdp2	**0.86**	0.07	-0.01
BTdp18	0.08	**0.86**	BTdp8	0.51	-0.32	**0.54**
NAOW1	**-0.56**	-0.08	BTdp18	-0.01	**0.85**	0.31
NAOW14	-0.37	**0.61**	NAOW11	-0.34	0.12	**-0.75**
HARP4	**-0.94**	0.03	NAOW16	**-0.60**	0.21	0.23
HARP18	0.13	**-0.90**	HARP3	**-0.94**	0.01	-0.10
EFF4	-0.02	**-0.90**	HARP4	**-0.94**	-0.07	-0.07
EFF9	**0.90**	0.10	HARP14	-0.18	0.19	**0.69**
			HARP17	-0.20	**-0.95**	-0.10
			EFF0	-0.17	0.30	**0.84**
			EFF4	0.04	**-0.90**	-0.16
			EFF8	**0.88**	0.06	-0.11

Table 7.2. Estimated regression parameters, standard errors and t-values for the relative abundance DFA model with 2 trends and 2 explanatory variables, fishing effort lagged 9 years and salinity lagged 11 years. For species codes, see text. **D** was explained in Chapter 2; $n = 14$.

	Fishing effort lagged 9 years			Salinity lagged 11 years		
Species	Estimated value **D**	Standard error	t-value	Estimated value **D**	Standard error	t-value
AP	0.42	0.11	3.66	0.06	0.11	0.58
AC	0.10	0.19	0.55	-0.05	0.20	-0.26
AW	0.54	0.11	5.01	0.19	0.12	1.61
BD	0.62	0.14	4.38	-0.24	0.19	-1.25
BH	0.43	0.15	2.82	-0.43	0.20	-2.13
DR	0.60	0.10	5.80	-0.12	0.13	-0.94
GR	0.19	0.17	1.07	0.03	0.20	0.13
GH	1.21	0.14	8.83	0.97	0.19	5.20
NW	0.47	0.10	4.71	-0.10	0.10	-1.04
RHD	0.46	0.11	4.14	-0.18	0.13	-1.34
RK	0.48	0.17	2.86	-0.24	0.23	-1.05
SS	0.37	0.11	3.19	-0.23	0.12	-1.90
SW	0.31	0.13	2.47	0.11	0.12	0.87
TS	0.24	0.20	1.18	0.23	0.25	0.91

Table 7.3. Values of Akaike's information criterion (AIC) for DFA models and different sets of explanatory variables (exp), based on a symmetrical, diagonal covariance matrix for relative abundance. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend model	–	289.7
2 trend model	–	290.9
Relative abundance + exp + noise		
2 trend model	Fishing effort lagged 9 years	235.6
2 trend model	Salinity lagged 11 years	242.9
1 trend model	Fishing effort lagged 9 years + salinity lagged 11 years	86.5
2 trend model	Fishing effort lagged 9 years + salinity lagged 11 years	**91.6**

Table 7.4. Estimated regression parameters, standard errors and t-values for the mean size DFA model with 2 trends and 2 explanatory variables, predation lagged 16 years and NAO winter index lagged 4 years. For species codes, see text. **D** was explained in Chapter 2; $n = 14$.

	Predation lagged 16 years			NAO winter index lagged 4 years		
Species	Estimated value **D**	Standard error	t-value	Estimated value **D**	Standard error	t-value
AP	-5.06	0.54	-9.43	-0.32	0.10	-3.15
AC	-1.62	0.85	-1.90	-0.07	0.17	-0.42
AW	-2.04	0.81	-2.52	-0.08	0.14	-0.59
BD	-1.80	1.02	-1.77	0.20	0.20	0.97
BH	-1.97	0.78	-2.53	0.02	0.13	0.18
DR	-4.11	0.95	-4.31	0.49	0.17	2.92
GR	0.74	1.12	0.66	0.64	0.25	2.56
GH	-1.71	0.71	-2.42	0.01	0.10	0.09
NW	-3.29	0.95	-3.47	-0.40	0.14	-2.86
RHD	-4.51	0.72	-6.28	0.13	0.13	0.98
RK	-0.88	1.13	-0.78	0.40	0.23	1.78
SS	-2.53	0.95	-2.67	0.09	0.20	0.46
SW	-4.98	0.54	-9.23	-0.16	0.10	-1.59
TS	-2.97	0.85	-3.48	0.28	0.16	1.72

Table 7.5. Values of Akaike's information criterion (AIC) for DFA models and different sets of explanatory variables (exp), based on a diagonal covariance matrix for mean size. Bold type indicates the best model chosen for the analysis.

Model	Explanatory variable (exp)	AIC
Relative abundance + noise		
1 trend model	–	499.9
2 trend model	–	432.6
3 trend model	–	411.1
Relative abundance + exp + noise		
2 trend model	Harp seal abundance lagged 16 years	411.1
2 trend model	NAO index lagged 4 years	429.0
1 trend model	Harp seal abundance lagged 16 years + NAO index lagged 4 years	499.7
2 trend model	Harp seal abundance lagged 16 years + NAO index lagged 4 years	**440.5**
3 trend model	Harp seal abundance lagged 16 years + NAO index lagged 4 years	446.3

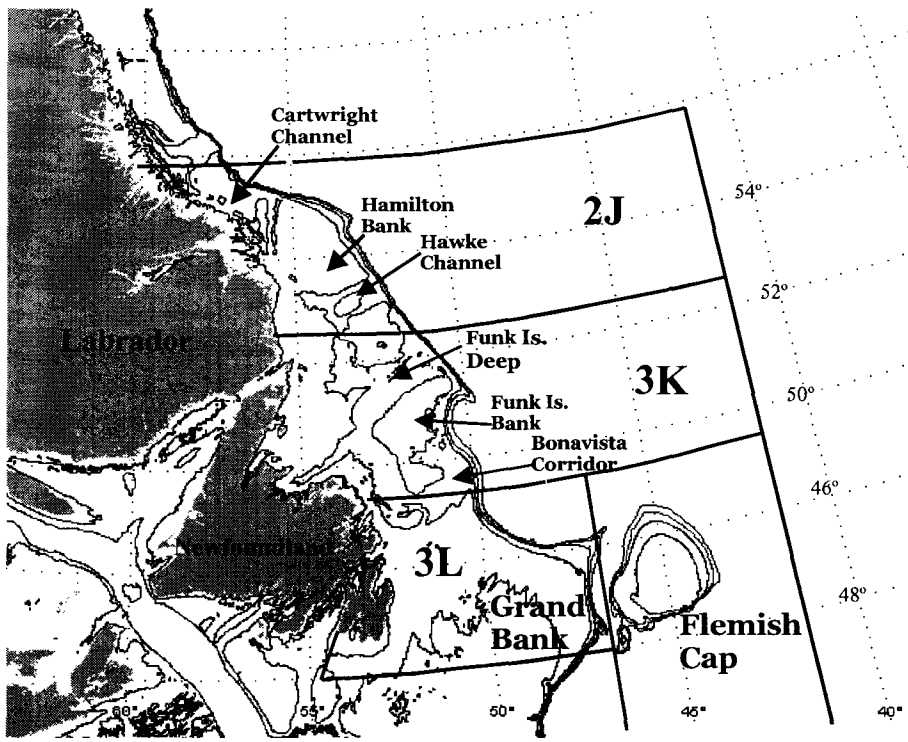

Figure 7.1. Newfoundland-Labrador Shelf system showing important banks, channels, and NAFO Areas 2J3KL. Contour lines depict 100, 300, 500, 700, and 900 meter contours.

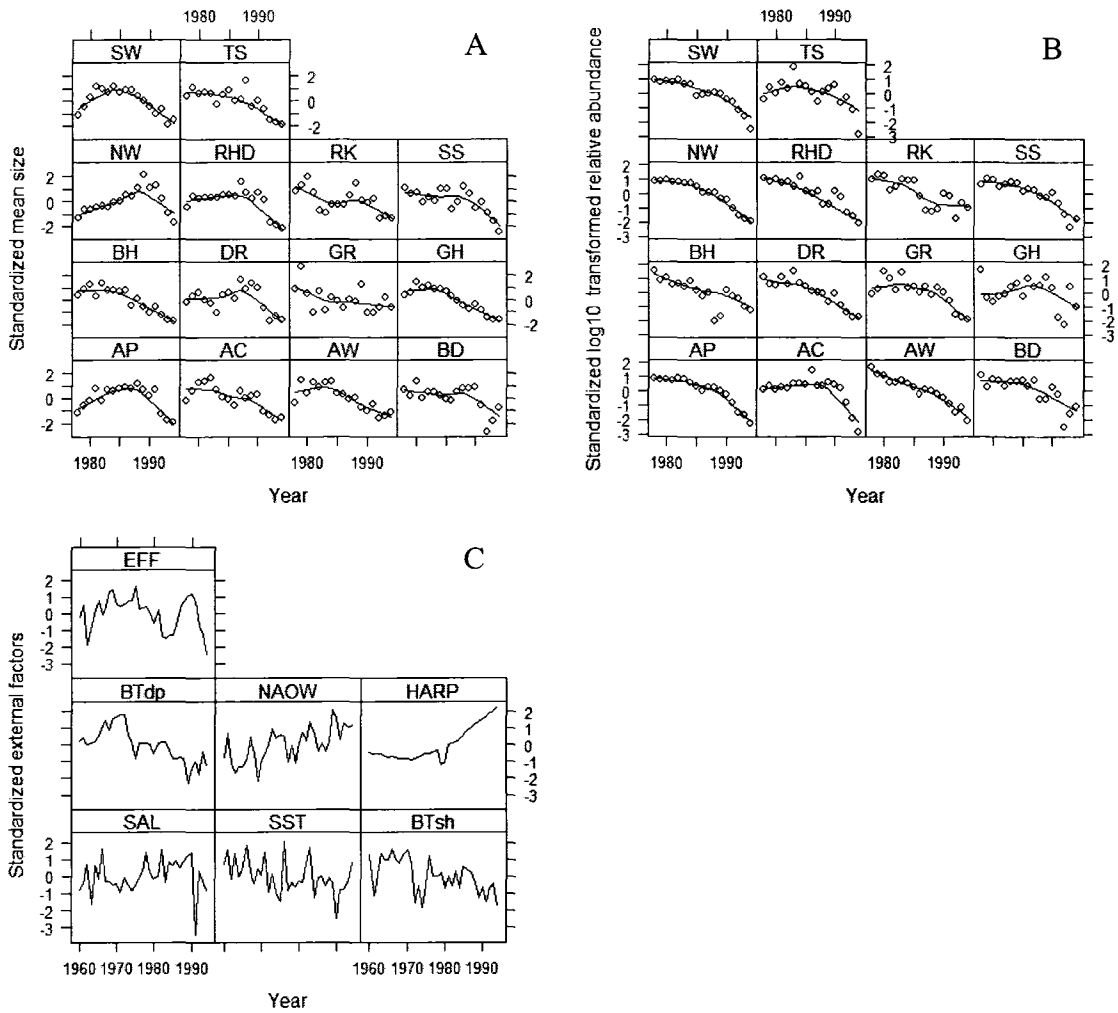

Figure 7.2. Lattice plots with smoothing lines of (A) mean size (kg per individual) 1978–1994, (B) relative abundance (weighted number per tow) 1978–1994, and (C) external factors 1960–1994 in NAFO Divisions 2J3KL. See text for abbreviations.

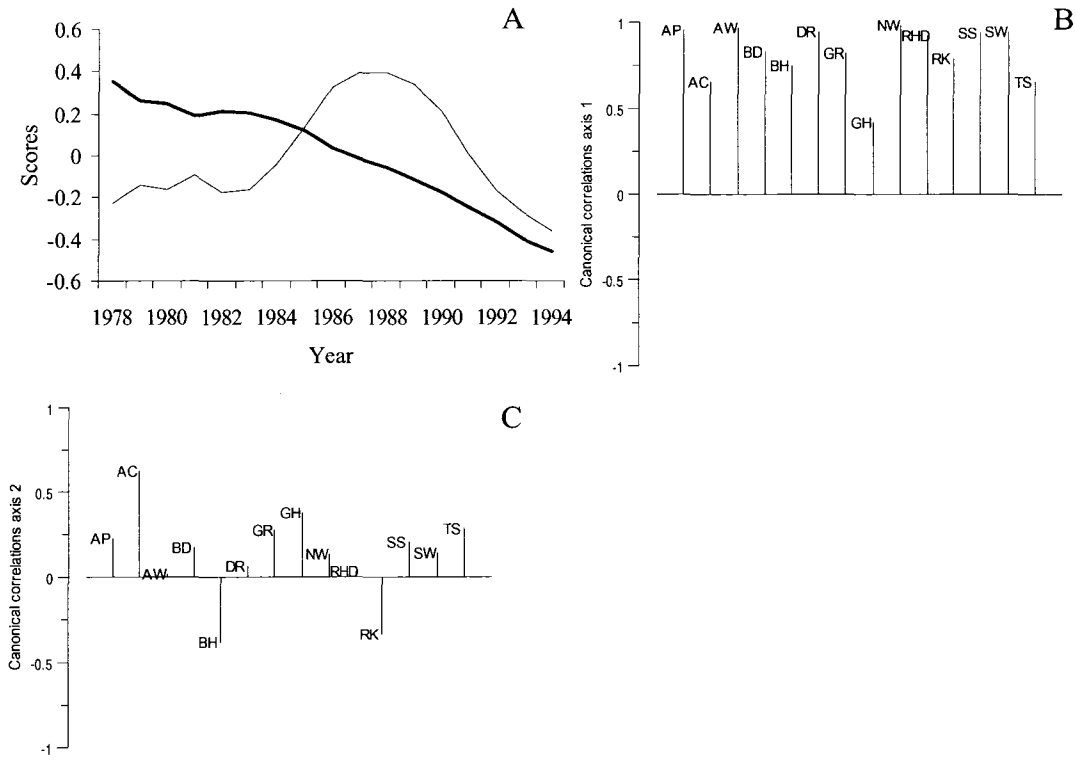

Figure 7.3. (A) MAFA trends in relative abundance (MAF1 = heavy line, MAF2 = thin line) and canonical correlations between species and (B) MAF1 or (C) MAF2. Significance level for all correlations is $r^2 \geq 0.49$. For species codes, see text.

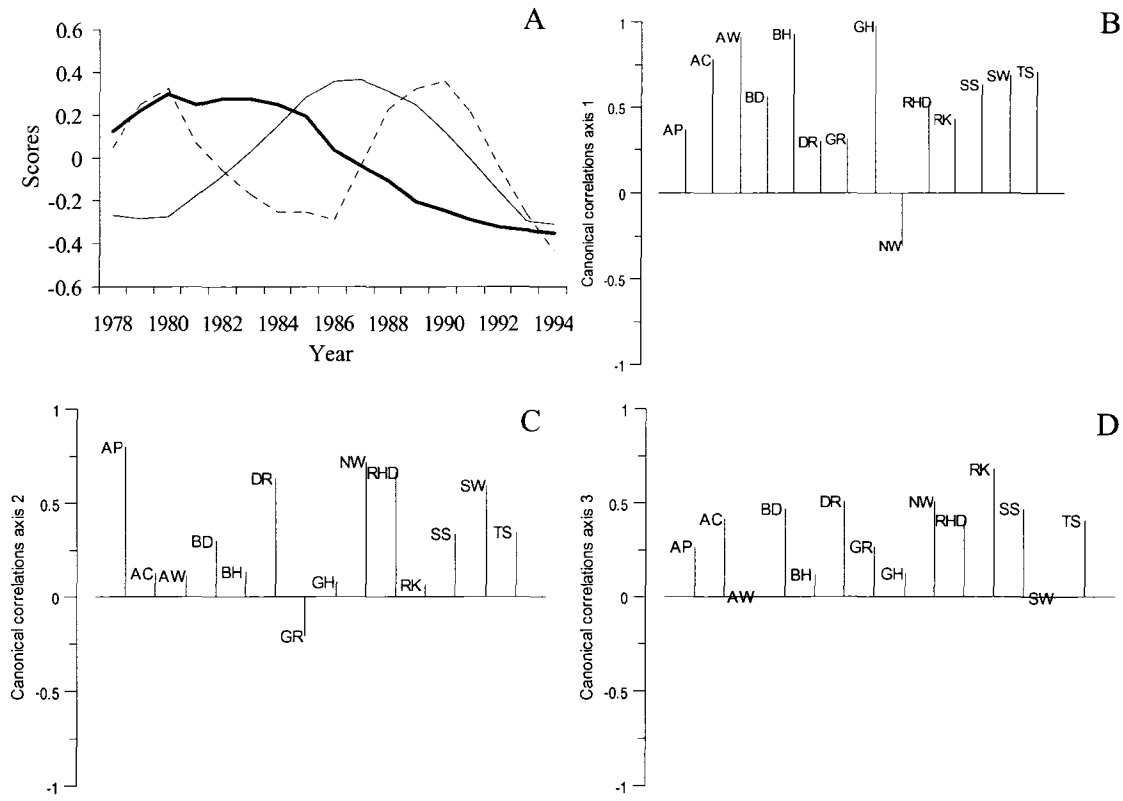

Figure 7.4. (A) MAFA trends in mean size (MAF1 = heavy line, MAF2 = thin line, MAF3 = dotted line) and canonical correlations for (B) MAF1, (C) MAF2, and (D) MAF3. Significance level for all correlations is $r^2 \geq 0.49$. For species codes, see text.

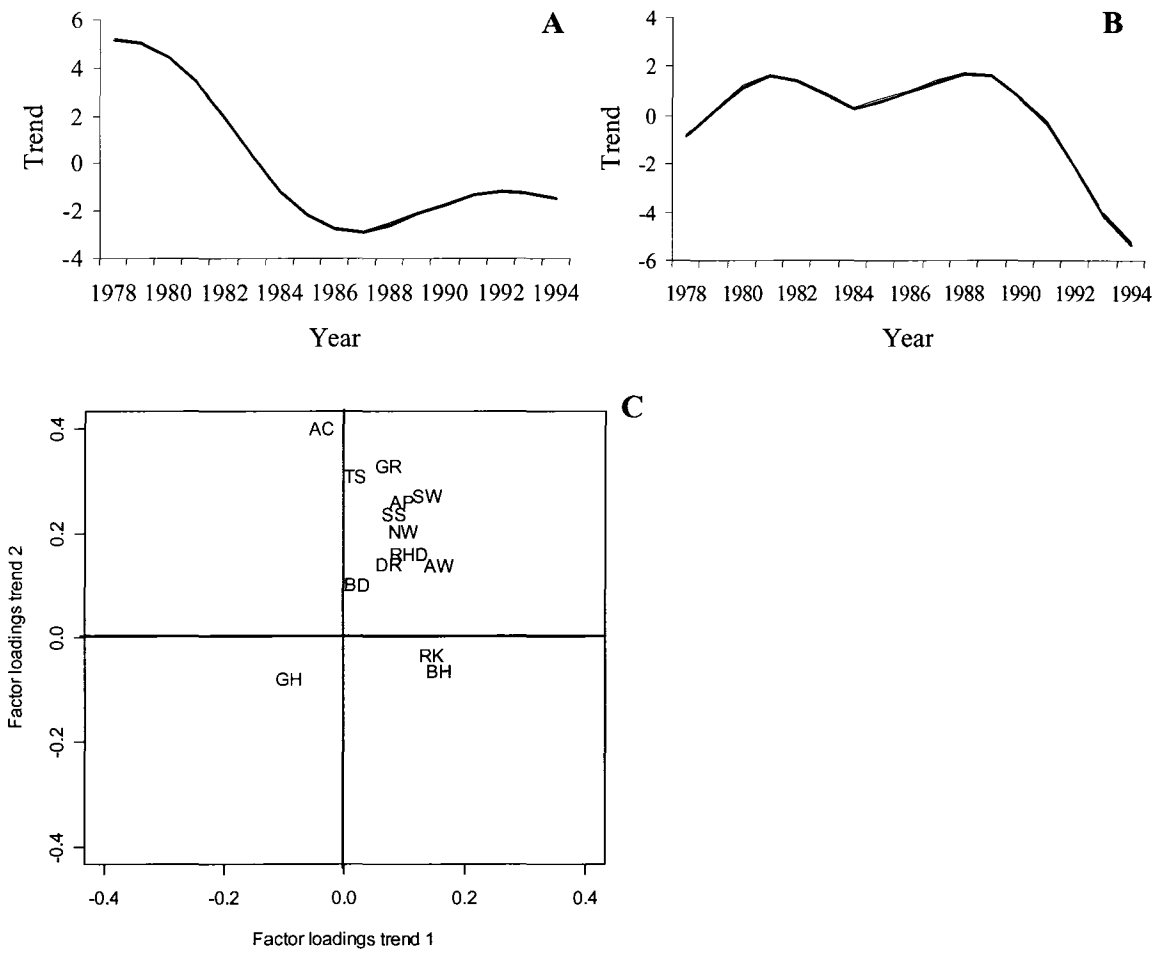

Figure 7.5. The first (A) and second (B) main trends with confidence intervals (very small intervals) for the DFA model with fishing effort lagged 9 years and salinity lagged 11 years for relative abundance of fourteen teleost and elasmobranch species in the Northwest Atlantic, NAFO Divisions 2J3KL, 1978–1994. (C) Biplot of DFA factor loadings indicating relationship between species and trends (for species codes, see text).

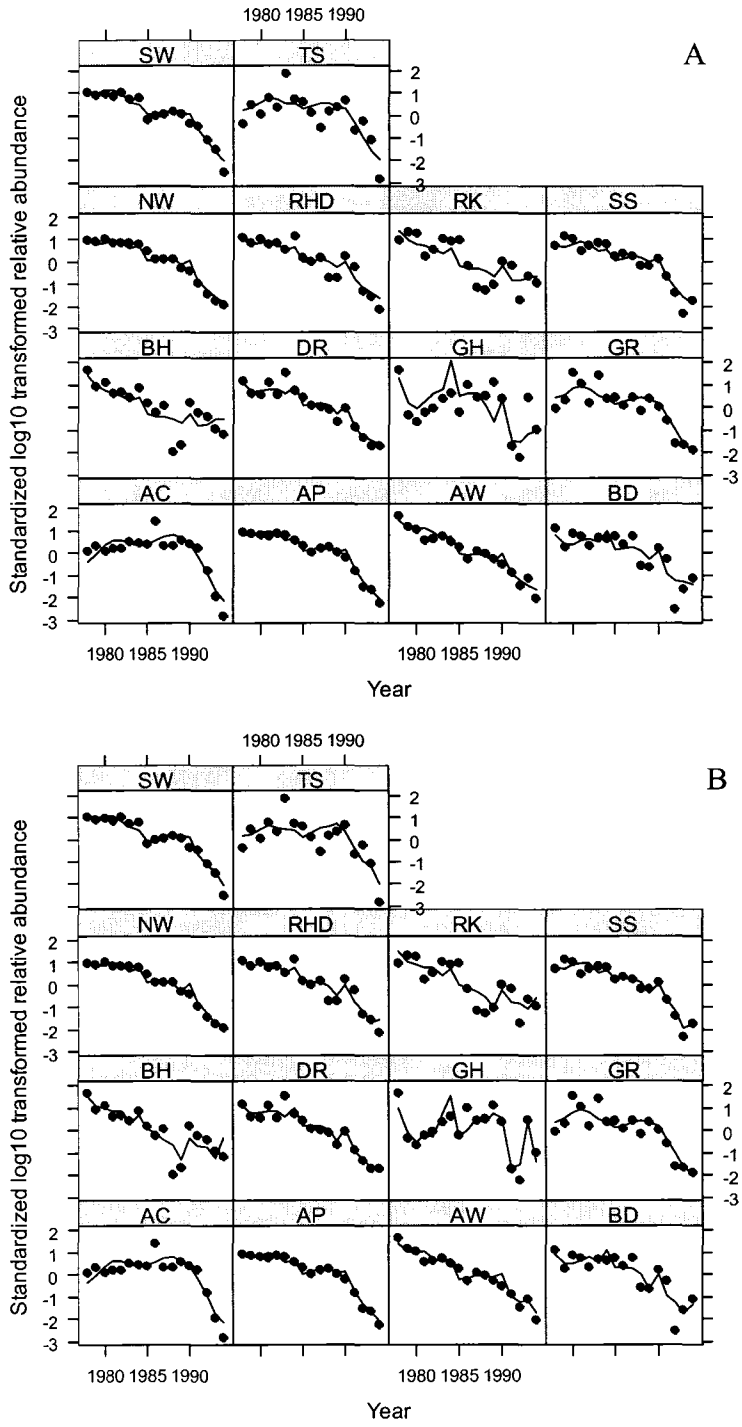

Figure 7.6. (A) Fit of model with 2 trend and 1 explanatory variable, fishing effort lagged 9 years, and (B) 2 trends and 2 explanatory variables, fishing effort lagged 9 years and salinity lagged 11 years, to relative abundance of 14 teleost and elasmobranch species in the Northwest Atlantic, NAFO Divisions 2J3KL, 1978–1994.

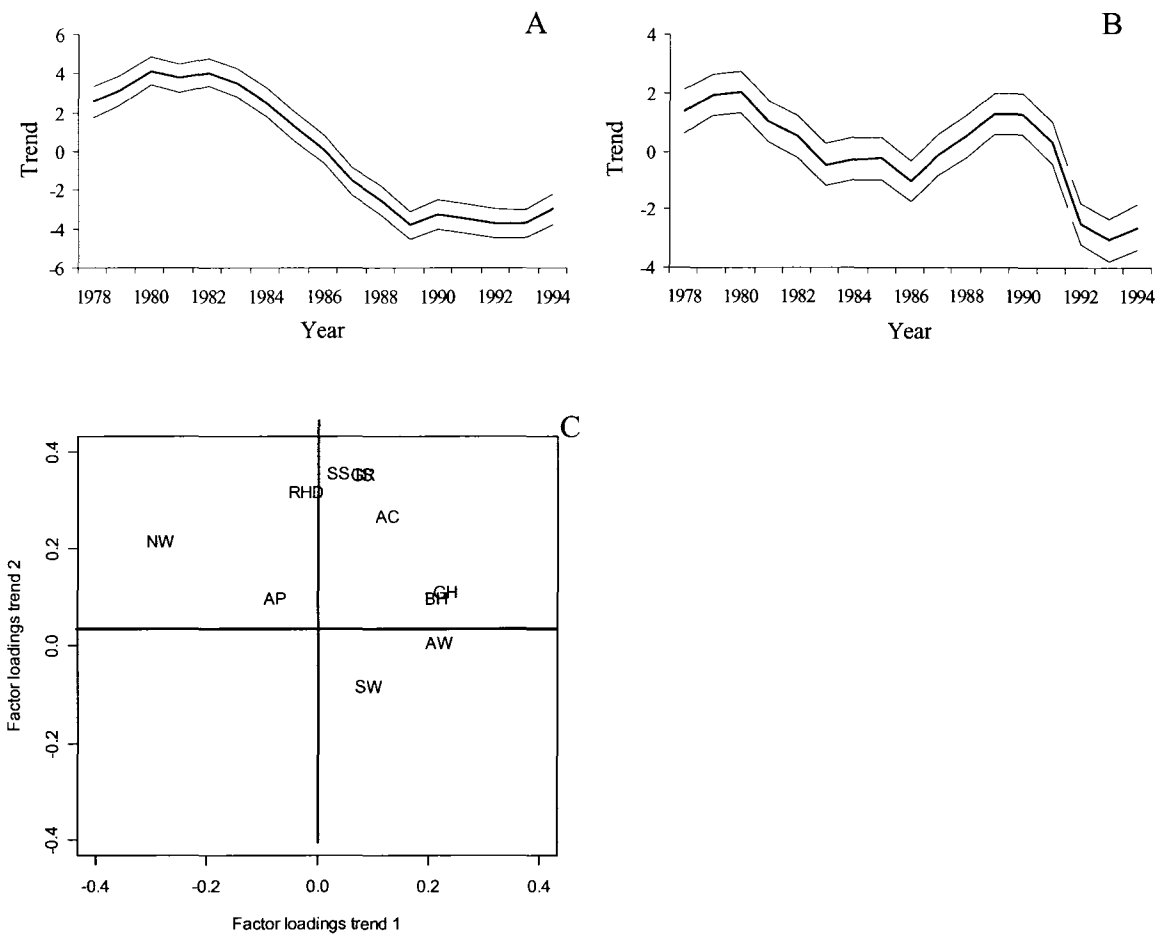

Figure 7.7. The (A) first and (B) second trends with confidence intervals for the DFA model with predation lagged 16 years and NAO winter index lagged 4 years in mean size of fourteen teleost and elasmobranch species in the Northwest Atlantic, NAFO Divisions 2J3KL, 1978–1994. (C) Biplot of DFA factor loadings indicating relationship between species and trends (for species codes, see text).

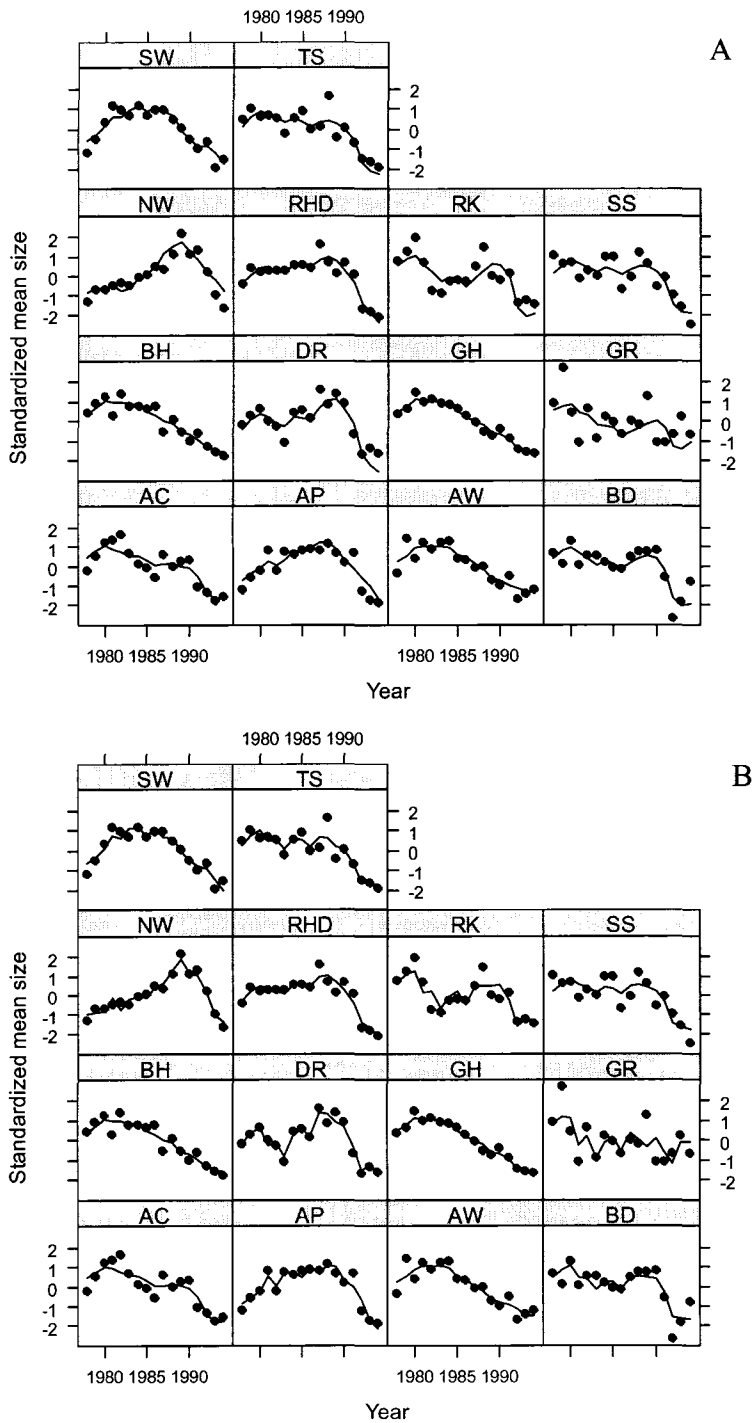

Figure 7.8. (A) Fit of model with 2 trend and 1 explanatory variable, predation lagged 16 years, and (B) 2 trends and 2 explanatory variables, predation lagged 16 years and the NAO winter index lagged 4 years, to mean size of 14 teleost and elasmobranch species in the Northwest Atlantic, NAFO Divisions 2J3KL, 1978–1994.

Appendix 7A. Fits of models to relative abundance.

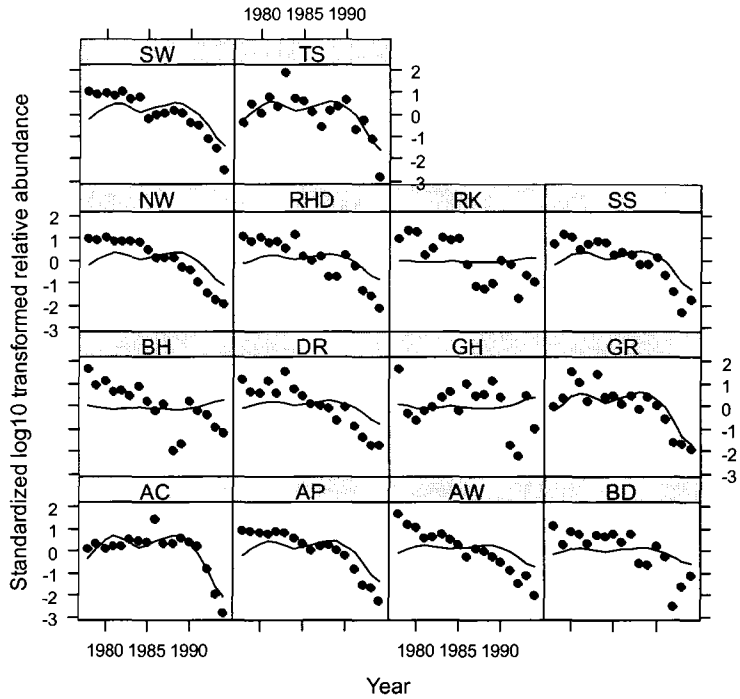

Figure 7A.1. Fit of constant + effect of the first trend to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

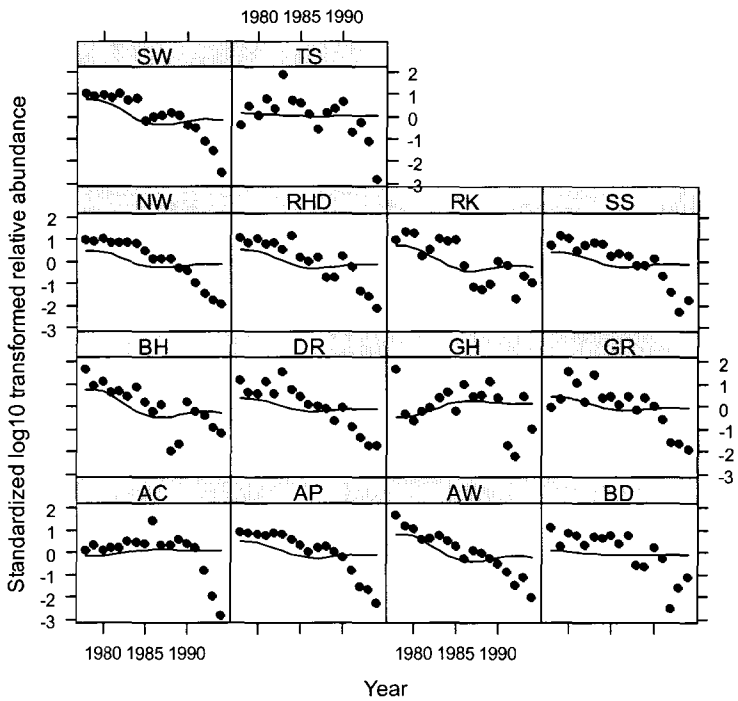

Figure 7A.2. Fit of constant + effect of the second trend to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

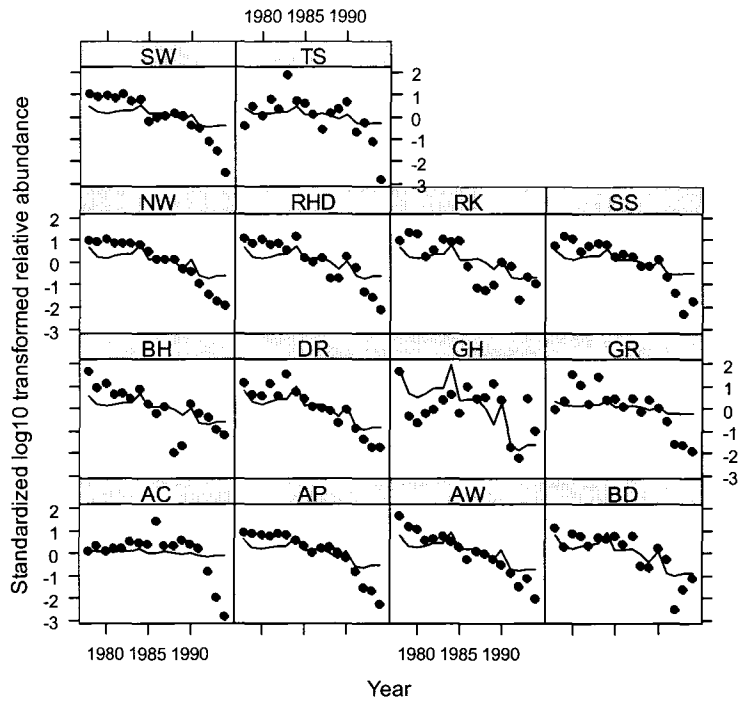

Figure 7A.3. Fit of constant + fishing effort lagged 9 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

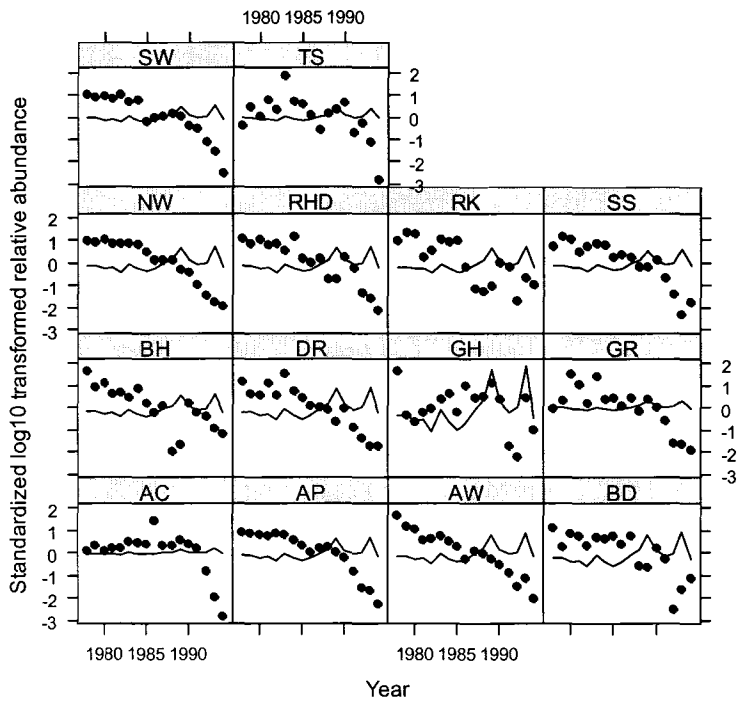

Figure 7A.4. Fit of constant + salinity lagged 11 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

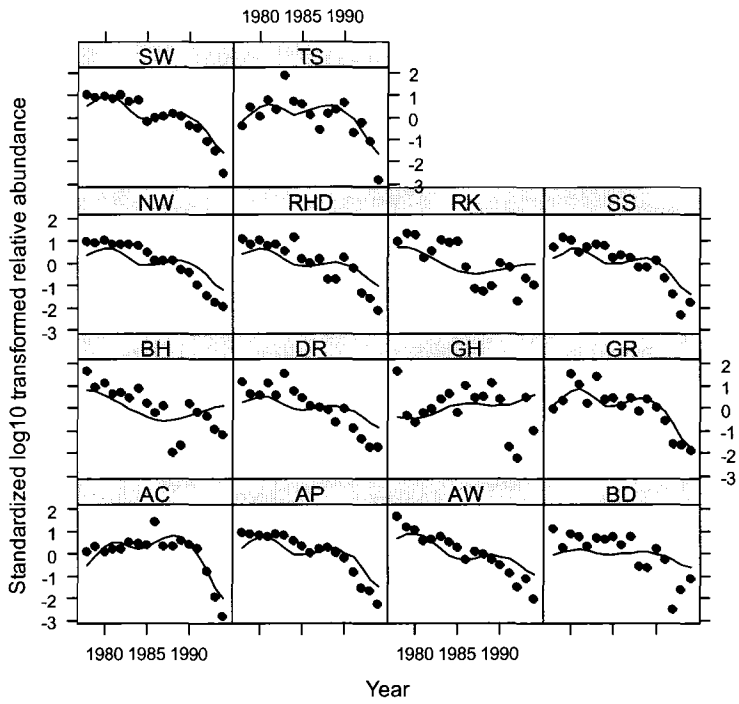

Figure 7A.5. Fit of constant + effect of the first trend + second trend to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

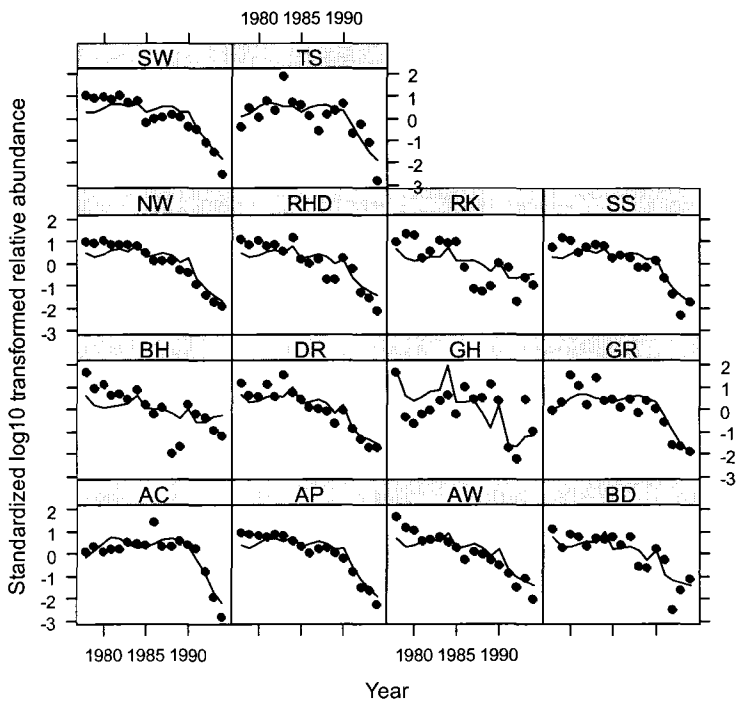

Figure 7A.6. Fit of constant + effect of the first trend + fishing effort lagged 9 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

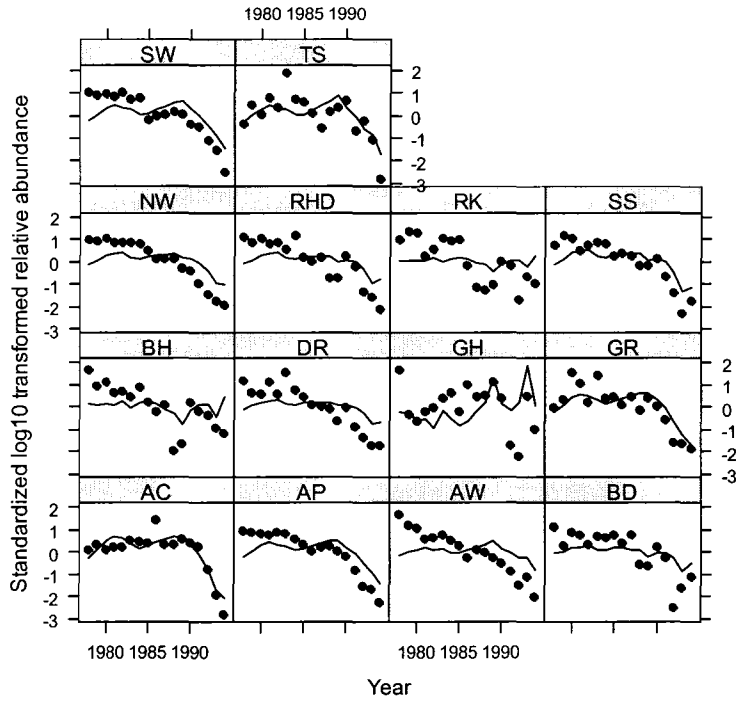

Figure 7A.7. Fit of constant + effect of the first trend + salinity lagged 11 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

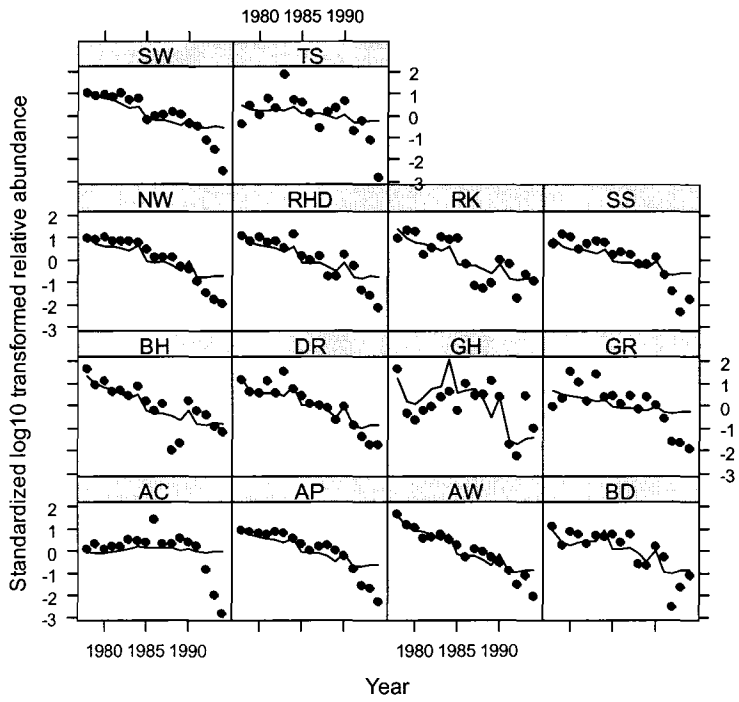

Figure 7A.8. Fit of constant + effect of the second trend + fishing effort lagged 9 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

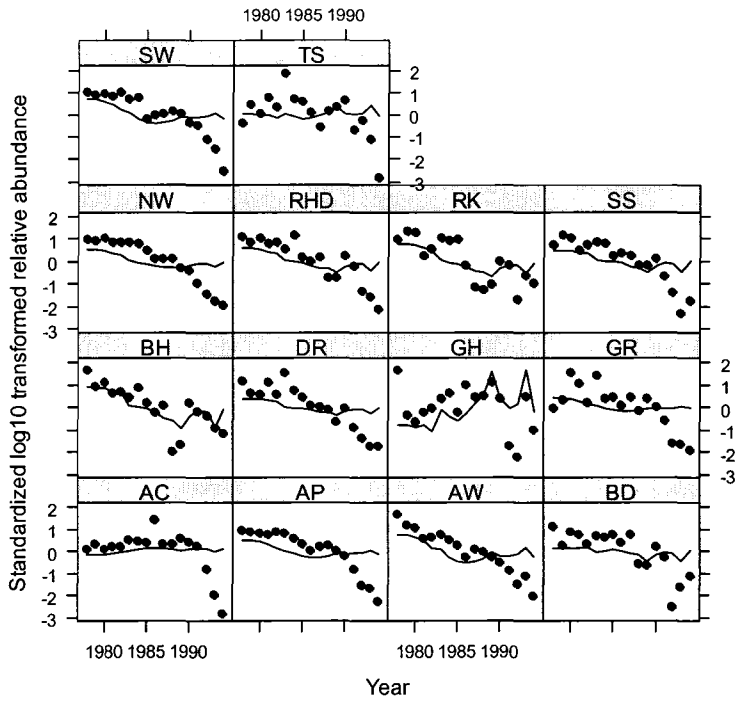

Figure 7A.9. Fit of constant + effect of the second trend + salinity lagged 11 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

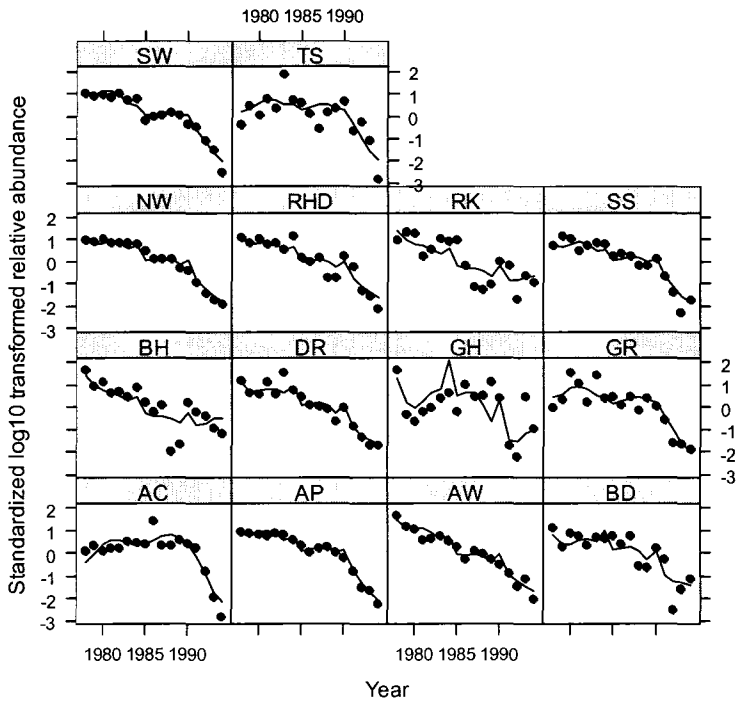

Figure 7A.10. Fit of constant + effect of first trend + effect of second trend + fishing effort lagged 9 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

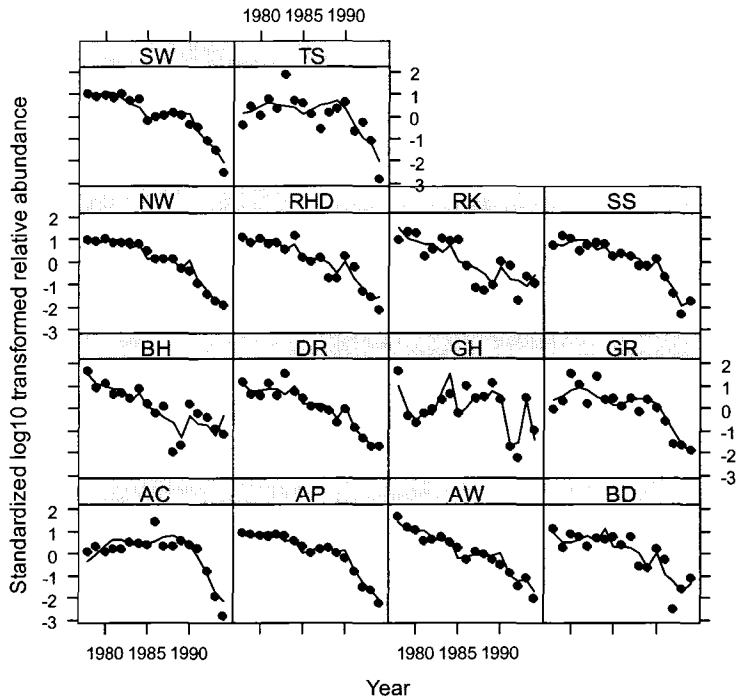

Figure 7A.11. Fit of constant + effect of first trend + effect of second trend + fishing effort lagged 9 years + salinity lagged 11 years to relative abundance in NAFO Divisions 2J3KL, 1978–1994.

Appendix 7B. Fits of models to mean size.

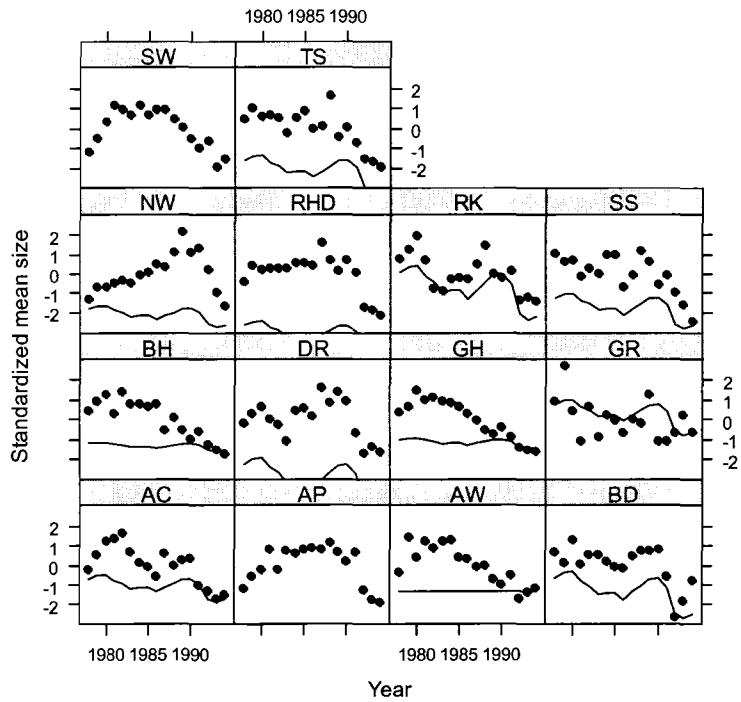

Figure 7B.1. Fit of constant + effect of the first trend to mean size in NAFO Divisions 2J3KL, 1978–1994.

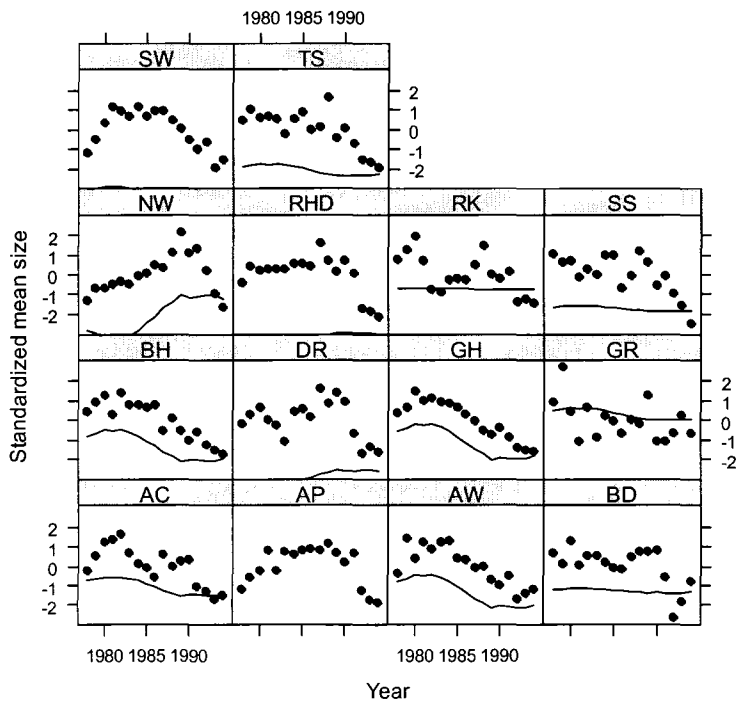

Figure 7B.2. Fit of constant + effect of the second trend to mean size in NAFO Divisions 2J3KL, 1978–1994.

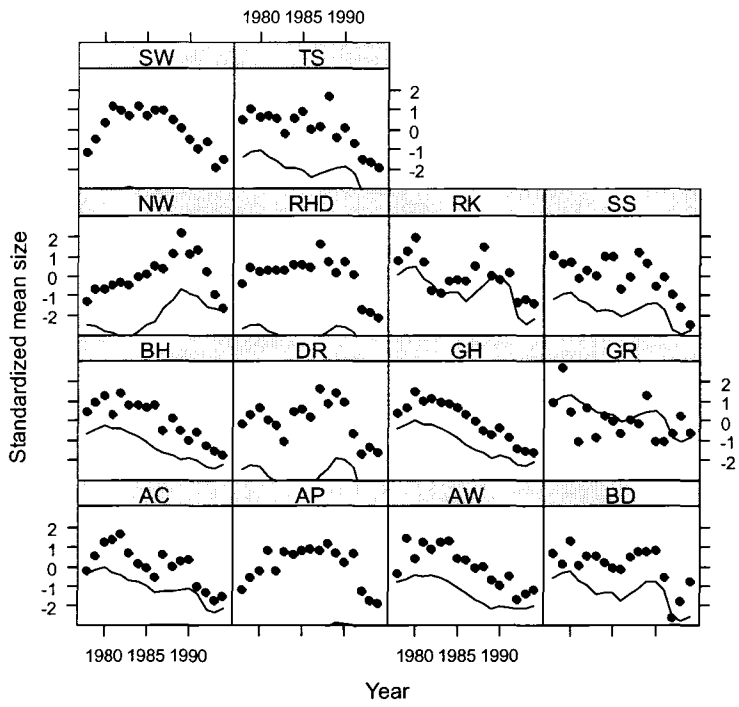

Figure 7B.3. Fit of constant + effect of the first trend + effect of the second trend to mean size in NAFO Divisions 2J3KL, 1978–1994.

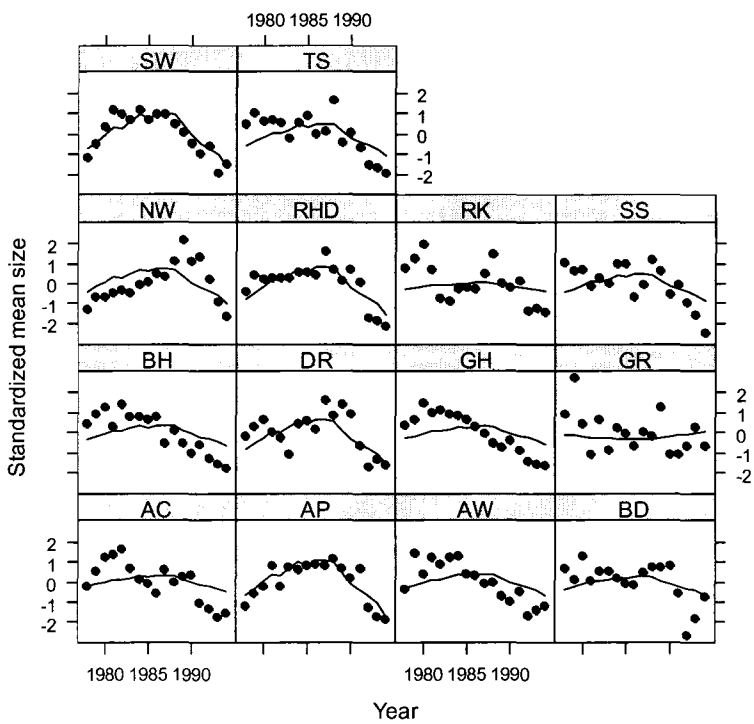

Figure 7B.4. Fit of constant + effect of predation lagged 16 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

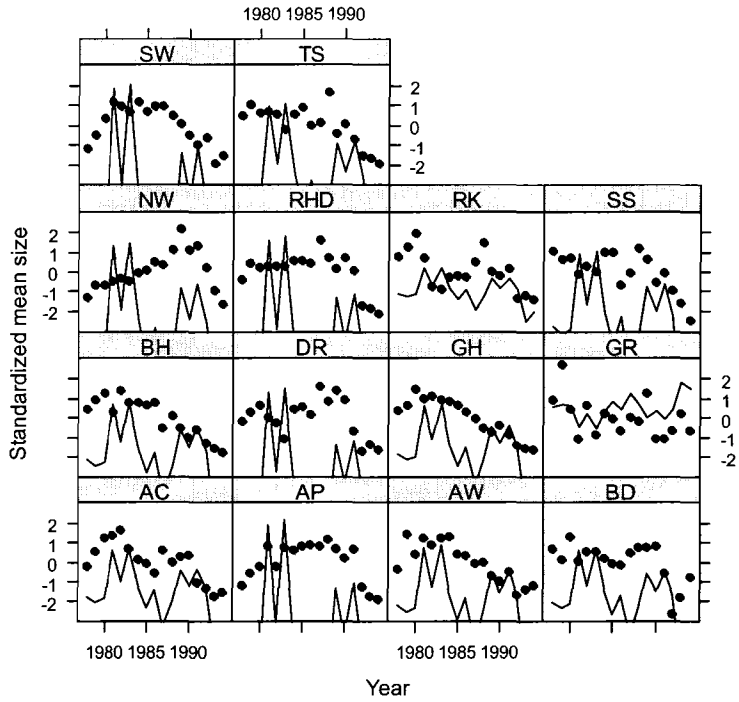

Figure 7B.5. Fit of constant + effect of the NAO winter index lagged 4 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

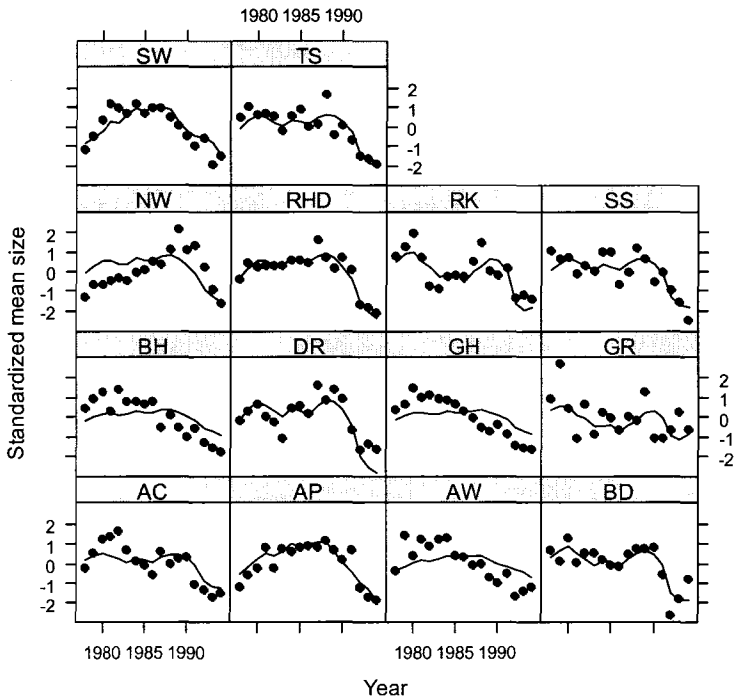

Figure 7B.6. Fit of constant + effects of the first trend + effect of predation lagged 16 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

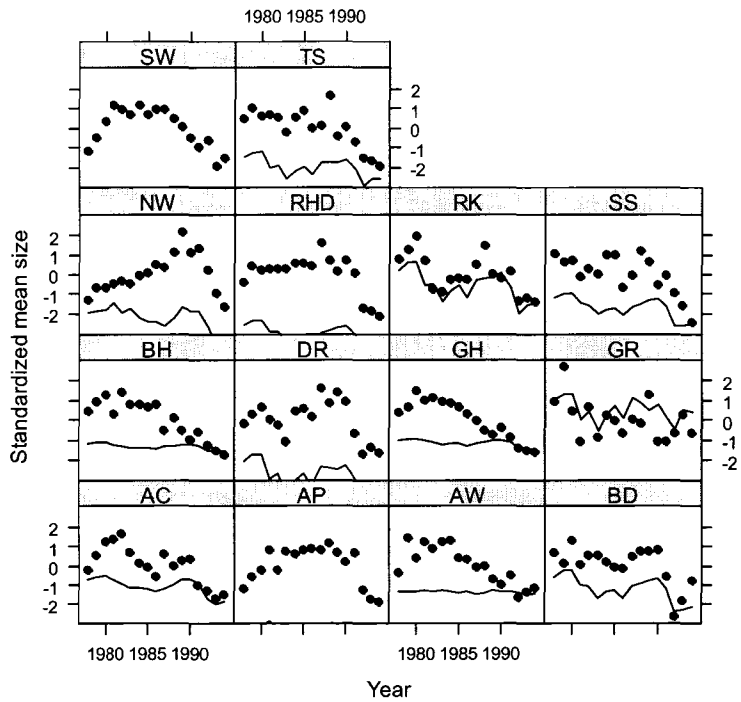

Figure 7B.7. Fit of constant + effect of the first trend + effect of the NAO winter index lagged 4 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

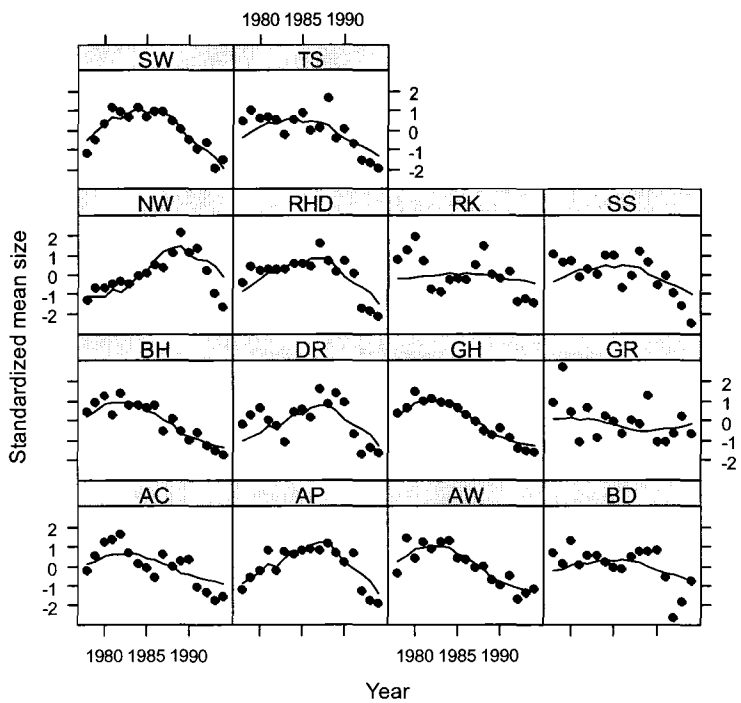

Figure 7B.8. Fit of constant + effects of the second trend + effect of predation lagged 16 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

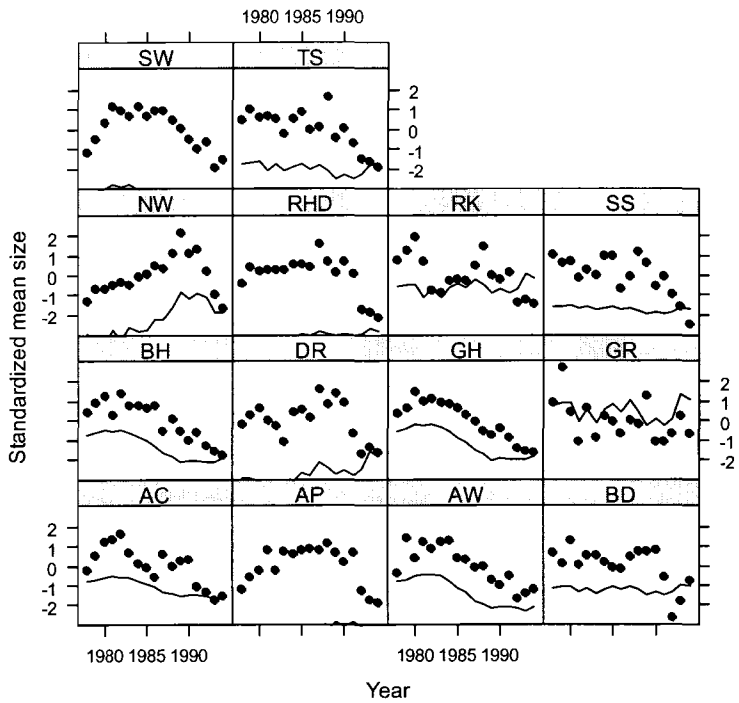

Figure 7B.9. Fit of constant + effect of the second trend + effect of the NAO winter index lagged 4 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

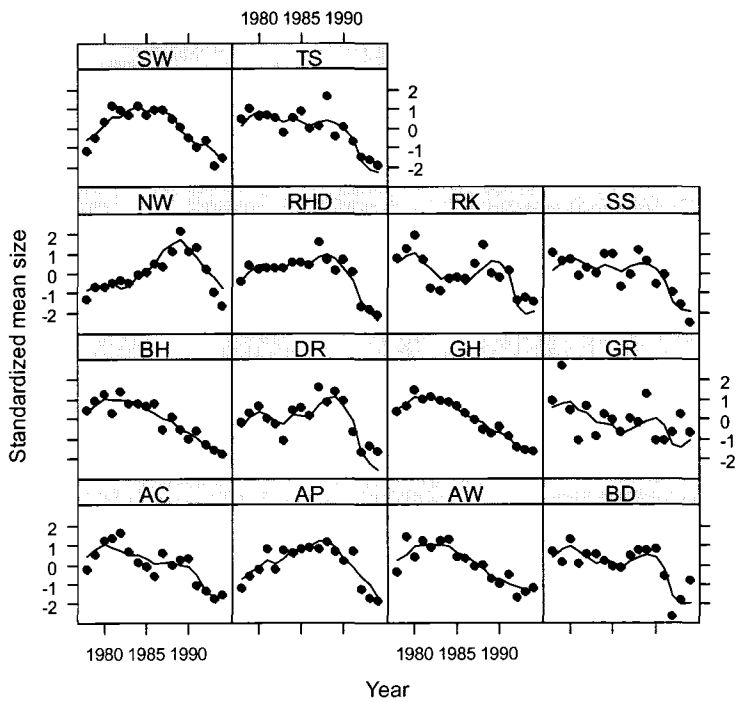

Figure 7B.10. Fit of constant + effect of the first trend + effect of the second trend + effect of predation lagged 16 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

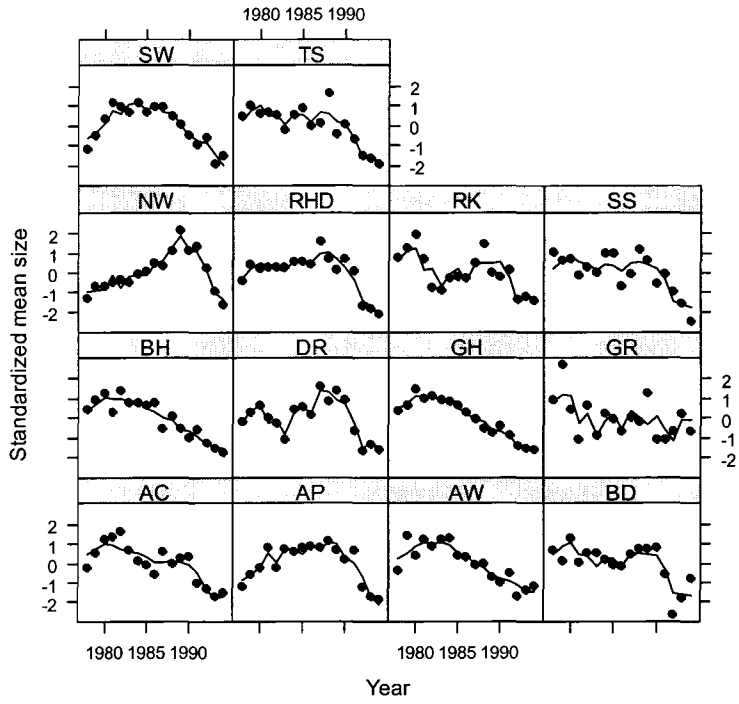

Figure 7B.11. Fit of constant + effect of the first trend + effect of the second trend + effect of predation lagged 16 years + effect of the NAO winter index lagged 4 years to mean size in NAFO Divisions 2J3KL, 1978–1994.

Appendix C. Raw data.

Table 1C. Time series of relative abundance for the fourteen species used in the analyses, 1978–1994. See Methods for abbreviations.

Year	AP	AC	AW	BD	BH	DR	GR	GH	NW	RHD	RK	SS	SW	TS
1978	167.01	31.61	5.27	0.59	1.56	224.42	0.61	46.94	1.70	4.48	7.95	0.12	0.86	5.34
1979	159.88	44.46	3.35	0.20	0.70	103.24	1.18	29.16	1.59	3.83	12.25	0.17	0.76	6.56
1980	151.20	33.29	2.97	0.43	0.84	93.64	12.75	26.69	1.74	4.28	11.65	0.16	0.81	5.97
1981	141.89	39.41	1.85	0.37	0.48	204.46	4.93	29.81	1.39	3.59	3.11	0.10	0.70	7.09
1982	161.58	36.47	1.94	0.22	0.53	99.55	1.00	31.26	1.38	3.84	4.58	0.12	0.86	6.40
1983	151.32	59.62	2.25	0.34	0.41	396.20	10.47	34.84	1.34	3.10	8.03	0.13	0.61	9.27
1984	115.31	54.84	1.73	0.33	0.66	123.71	1.31	36.94	1.24	4.74	7.27	0.13	0.64	6.93
1985	90.51	49.72	1.41	0.38	0.32	82.32	1.50	30.03	0.86	2.35	7.57	0.08	0.25	6.74
1986	64.54	208.38	0.84	0.23	0.20	48.41	0.75	40.17	0.48	2.08	1.76	0.09	0.29	6.05
1987	80.05	44.29	1.18	0.36	0.26	45.32	1.65	35.26	0.48	2.39	0.49	0.08	0.32	5.12
1988	86.50	45.51	1.07	0.07	0.03	38.67	0.48	35.87	0.49	1.26	0.43	0.06	0.34	6.09
1989	64.29	61.65	0.86	0.07	0.04	16.45	1.38	41.43	0.27	1.24	0.57	0.05	0.32	6.39
1990	50.68	49.76	0.69	0.19	0.31	42.15	0.68	34.31	0.22	2.45	2.23	0.07	0.20	6.83
1991	26.56	36.38	0.47	0.11	0.20	12.08	0.22	20.71	0.10	1.79	1.75	0.04	0.18	5.00
1992	12.81	9.41	0.27	0.01	0.16	5.86	0.03	18.28	0.05	0.83	0.24	0.02	0.09	5.51
1993	10.76	1.94	0.38	0.02	0.08	3.60	0.03	34.97	0.03	0.70	0.92	0.01	0.06	4.47
1994	5.88	0.59	0.16	0.04	0.07	3.54	0.02	24.50	0.03	0.48	0.61	0.01	0.02	2.97

Table 2C. Time series of mean size for the fourteen species used in the analyses, 1978–1994. See Methods for abbreviations.

Year	AP	AC	AW	BD	BH	DR	GH	GH	NW	RHD	RK	SS	SW	TS
1978	0.29	1.33	0.91	1.65	0.28	0.40	1.24	0.74	5.76	0.71	0.39	9.52	3.30	1.52
1979	0.33	1.66	1.19	1.52	0.32	0.44	1.57	0.80	6.87	0.82	0.44	8.71	3.85	1.82
1980	0.36	1.96	1.02	1.82	0.34	0.46	1.17	1.00	6.87	0.79	0.52	8.80	4.51	1.61
1981	0.43	2.01	1.16	1.48	0.27	0.41	0.89	0.88	7.17	0.80	0.38	7.21	5.22	1.65
1982	0.36	2.15	1.10	1.62	0.35	0.40	1.20	0.92	7.42	0.81	0.22	8.08	5.02	1.58
1983	0.42	1.71	1.15	1.62	0.30	0.33	0.93	0.87	7.13	0.80	0.20	7.52	4.81	1.18
1984	0.41	1.48	1.17	1.53	0.31	0.45	1.12	0.86	7.88	0.84	0.27	9.46	5.23	1.55
1985	0.43	1.36	1.03	1.45	0.30	0.46	1.07	0.81	8.03	0.83	0.28	9.45	4.82	1.73
1986	0.43	1.16	1.01	1.44	0.31	0.43	0.97	0.72	8.71	0.82	0.27	6.10	5.01	1.29
1987	0.43	1.70	0.95	1.59	0.21	0.54	1.09	0.64	8.58	0.98	0.35	7.31	5.02	1.35
1988	0.45	1.41	0.96	1.67	0.26	0.48	1.05	0.53	9.73	0.86	0.47	9.82	4.62	2.14
1989	0.42	1.52	0.85	1.68	0.21	0.52	1.31	0.47	11.42	0.79	0.30	8.72	4.28	1.09
1990	0.38	1.55	0.81	1.70	0.17	0.49	0.89	0.55	9.74	0.86	0.28	6.40	3.87	1.32
1991	0.42	0.96	0.89	1.33	0.21	0.36	0.89	0.44	10.07	0.78	0.32	7.31	3.44	0.95
1992	0.28	0.83	0.71	0.78	0.16	0.28	0.97	0.30	8.29	0.54	0.14	5.52	3.73	0.52
1993	0.25	0.65	0.74	1.00	0.13	0.31	1.12	0.26	6.41	0.52	0.16	4.26	2.68	0.44
1994	0.24	0.73	0.78	1.27	0.12	0.29	0.97	0.26	5.22	0.48	0.14	2.51	2.99	0.33

Table 3C. Time series of explanatory variables, 1960–1994. See Methods for abbreviations.

Year	SAL	SST	250–500 BT	500–1485 BT	NAO	HARP	EFF
1960	-0.31	0.28	0.79	0.37	-1.54	2181296	21777
1961	-0.17	0.55	-0.53	0.53	1.80	2094780	26973
1962	0.30	0.02	0.11	0.19	-2.38	2144758	10096
1963	-0.67	0.48	0.80	0.26	-3.60	2080586	18753
1964	0.29	0.06	0.61	0.39	-2.86	2006055	24940
1965	-0.05	0.17	0.62	0.58	-2.88	1930035	29308
1966	0.69	0.65	0.96	1.04	-1.69	1947211	22939
1967	-0.11	0.16	0.63	1.23	1.28	1883240	26492
1968	-0.10	-0.06	0.52	0.81	-1.04	1809676	33456
1969	-0.19	0.20	0.81	1.31	-4.89	1849494	33785
1970	-0.16	0.09	0.92	1.38	-1.89	1798015	27493
1971	-0.35	0.52	0.50	1.47	-0.96	1794518	26427
1972	-0.02	-0.21	-0.76	1.47	0.34	1812690	27740
1973	-0.20	0.12	-0.23	0.61	2.52	1921058	28968
1974	-0.32	-0.20	-0.92	0.29	1.23	2023937	29082
1975	-0.23	-0.39	-0.19	-0.39	1.63	2099010	35497
1976	-0.01	0.71	0.74	0.25	1.37	2150462	25642
1977	0.15	-0.18	0.09	0.25	-2.14	2217890	26015
1978	0.61	-0.04	0.09	0.24	0.17	2339198	26260
1979	0.11	-0.13	0.20	0.21	-2.25	1463715	23421
1980	-0.05	-0.01	-0.30	-0.19	0.56	1594378	19066
1981	0.03	-0.04	0.09	0.25	2.05	2717783	24876
1982	0.67	0.30	-0.22	0.32	0.80	2746727	13457
1983	-0.14	0.61	0.22	0.34	3.42	2814478	12362
1984	0.38	-0.32	-0.31	-0.01	1.60	3001262	13818
1985	0.27	0.06	0.40	-0.38	-0.63	3207097	13824
1986	0.40	0.08	0.32	-0.41	0.50	3440787	18268
1987	0.22	-0.11	0.20	-0.35	-0.75	3674108	25447
1988	0.38	0.05	-0.10	-0.41	0.72	3876380	28504
1989	0.51	-0.04	-0.61	-1.47	5.08	4044171	31331
1990	0.56	-0.71	-0.26	-0.78	3.96	4175464	31778
1991	-1.42	-0.18	-0.70	-0.53	1.03	4341301	28680
1992	0.14	-0.17	-0.28	-1.10	3.28	4531699	17497
1993	-0.09	-0.01	-0.15	-0.12	2.67	4672646	14041
1994	-0.35	0.31	-0.84	-0.70	3.03	4877703	5676

Chapter 8. That's All

Rice (2002) lamented the inability to fully explore the dynamics of the Newfoundland Shelf, a large marine ecosystem, because of the lack of time series data on many of the biological components. The decision in 1995 to change survey gears to increase the capture of small fish and then to only calibrate the survey indices for a handful of commercially important species has severely eroded the amount of information available to study this system. Calibration studies for more species should be completed to recover historical (pre-1995) data. The data collected for the Northwest Atlantic does have limitations; however, the recent development of non-traditional, objective, exploratory time-series methods now allows for a rigorous examination of dynamics in this system.

In the introductory chapter, I described several important factors that must be considered when determining how change manifests itself in an ecosystem: 1) finding the causal factor(s) can be difficult, 2) indirect effects may mask the true causal factor(s), 3) the response of the system may operate on time lags, 4) the entire system or only parts can be affected differently and significantly because of relationships between processes, 5) longer temporal processes become increasingly important with increasing spatial scale of the system, and 6) biological components tend to react on different scales than do physical components (Francis et al. 1998, Rapport et al. 1998, Turner and Johnson 2001, Wootton 2002, Beaugrand 2004, Collie et al. 2004).

No one factor fully explains fish population and community dynamics in the Northwest Atlantic, but rather a combination of factors are largely responsible for the dynamics seen today. Finding the causal factors has indeed been difficult and, although

the main factors (exploitation, environment and natural predation) were explored here, some of the possible ecological mechanisms potentially responsible for indirect effects, such as competition or food availability, were not explored. Nevertheless, I have shown that exploitation, environment and natural (non-human) predation are important factors for many of the trends in the demersal and deep-sea fish community. In only a few cases did the analyses suggest that there was information left unexplained by the factors focused on here; adding the missing link – food – may have resolved some of this information.

In addition to multiple factors acting in combination, factors operating on different temporal scales were particularly important. This was true regardless of the biological level (species, population, or community) used to examine the system (Figure 8.1). Although studies have shown different patterns exist over different spatial and temporal scales (e.g., Steele 1989, Flach 1996, Turner et al. 2003, deYoung et al. 2004a,b), it was difficult to determine if this variability was true for the demersal community, deep-sea or redfish populations examined here. The situation is quite complex. For the deep sea, factors tend to be important at longer temporal scales (> 9 years), especially for exploitation, most likely as a result of the life-history characteristics of these species (Gordon et al. 1995, Koslow 1996). However, a different range of scales was important for redfish, another long-lived, slow-growing species with low fecundity. At the fish community level, multiple factors operate over a wide range of temporal scales. When additional species with different life-history characteristics are included in the analysis, the temporal scale over which environmental factors range changed.

Within populations of the same species, different factors and different scales were found to be important (e.g., longer temporal scales seem to be more important for one species of grenadier than another). I have shown that different factors on different temporal scales affect the same species (*Sebastes*), even though the populations are adjacent, are not genetically distinct, and show similar trends. I found explanatory factors were important on different scales even according to lifestages; for juveniles, environmental factors operating on a short temporal scale are important, while longer scales were more important for adults. MAFA and DFA have been used to explore dynamics in fisheries ecosystems (Solow 1994, Gaertner et al. 1999, Zuur et al. 2003a,b, CIESM 2004, Zuur and Pierce 2004, Erzini et al. 2005); time lags, however, have only been considered in a few other studies to date using these methods (Erzini 2005, Devine et al. 2007, Erzini et al. 2007).

Although many studies have shown different patterns occur at different scales (e.g., Csirke 1995, Flach 1996, Spencer and Collie 1997, Wilbanks and Kates 1999, Schneider 2001), I did not find any evidence that longer temporal scales become more important with increasing spatial extent; long temporal scales were important at both the population and community levels. This difference may be because my smallest biological unit, a redfish population, already was distributed over a relatively large area (e.g., 185,000 km^2 for the Scotian Shelf alone).

There is a growing call for management at the ecosystem scale (NMFS 1999, NOAA 1996, NRC 1999, Link 2002a,b, Sinclair et al. 2002, Pikitch et al. 2004) and many models are available that attempt to capture the dynamics of the system (e.g., Carpenter et al. 1985, Radford and Blackford 1996, Loukos et al. 2003, Robinson and Frid 2003). Some

attempt to take into consideration the system's past (Daan 1980, Latour et al. 2003), but many are built to model future states of the system based on current or potential stresses (e.g., Pauly et al. 2000, 1999). Ecosystem models are useful for providing insights into a system and for indicating changes; ecosystem complexity should not deter their use (Fulton et al. 2003). Many models are not built to consider time lags within the system even though time lags play a large role in determining the future state. The future state of the system is not solely because of current situation and stresses, but more commonly is a response to those that occurred 5, 10, 15 or even more years ago.

I have not explored the full capabilities of MAFA and DFA here. It would be extremely interesting to add more components of the ecosystem to the model, such as pelagic species and large predators, such as marine mammals. Unfortunately, these methods can only cope with approximately twenty time series of response variables, limiting their abilities to explore full ecosystem dynamics. Relationships between species (response variables) can be explored with the correlation covariance matrix; high values indicate these elements have residual patterns in common that are not explained by common trends or explanatory variables (A. Zuur, Highland Statistics, personal communication). This could be one method to explore the out-of-phase cyclic patterns observed for two populations of *Sebastes fasciatus* and *S. mentella* on the Grand Bank or look for interactions that might be important within the demersal community. DFA can also be used for forecasting (Zuur et al. 2003b). The redfish data would be ideal for this purpose because the time series for environmental and exploitation factors is slightly longer than the abundance time series for some populations; these data could be used to

check the predicted trends in abundance and validate the model before forecasting forward in time.

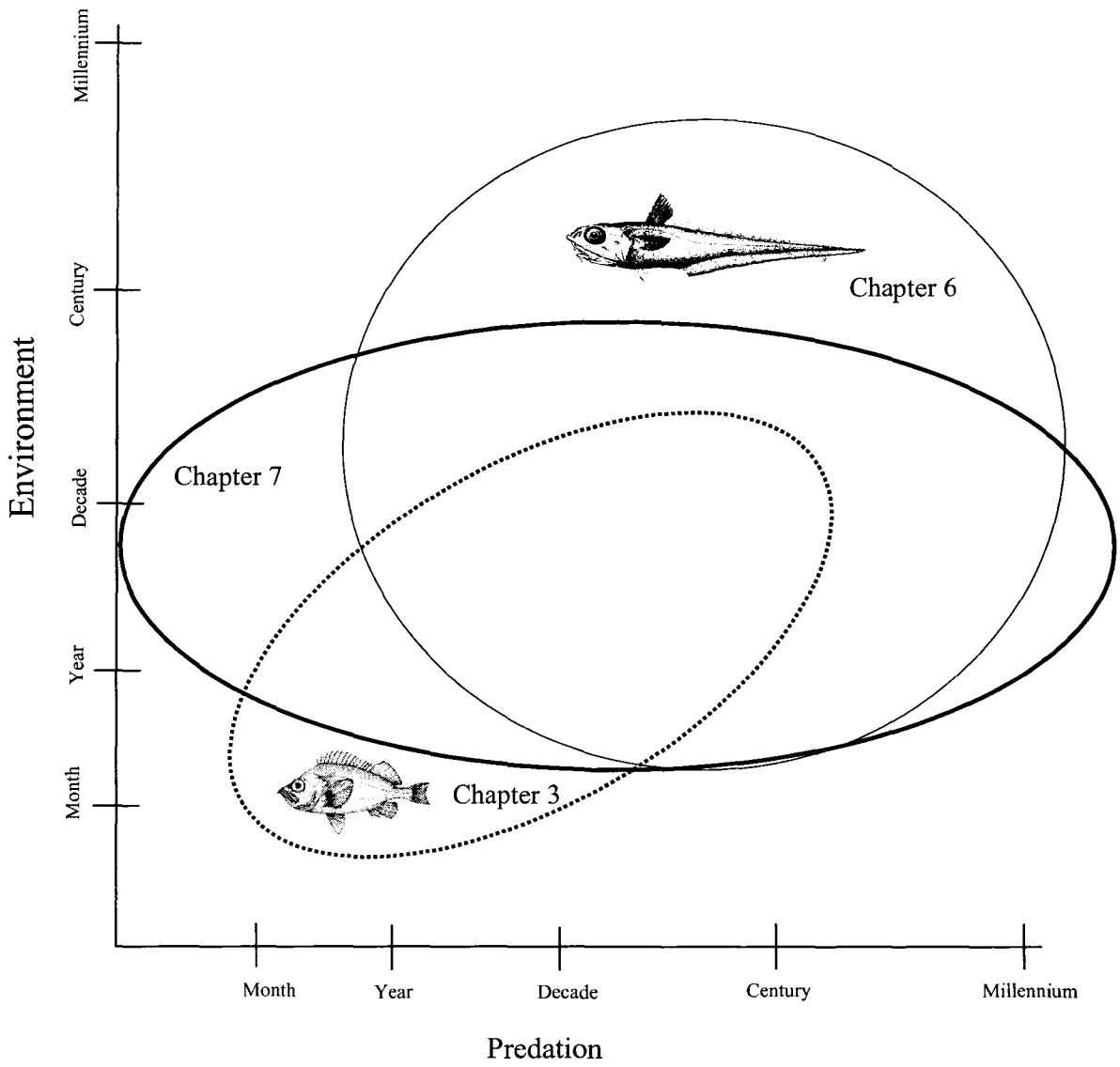

Figure 8.1. Temporal scale over which fish species, populations and communities operate in the Northwest Atlantic. Predation included exploitation and natural predation. Thick line = community; thin line = deep-sea, and dotted = redfish. Axes are on log scales.

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